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CELLULAR CHANGES IN RELATION TO RUST RESISTANCE¹

By F. S. THATCHER²

Abstract

Concomitant studies of the histopathological development and permeability changes associated with the browning reaction of Kubanka wheat to *Puccinia graminis Tritici* race 34 shows that the browning symptom is caused by encystment of haustoria and brown discoloration of host cell walls. This reaction is accompanied by a progressive permeability increase of host cells to a degree that probably becomes fatal.

Extremes of resistance and of susceptibility manifest in the mesothetic reaction are found to be associated, respectively, with local decrease and increase of solute permeability of the host cell membrane.

Cold hardening of wheat plants under some conditions caused a more vigorous development of rust and a slight lessening of resistance symptoms, actions that may be associated with a permeability increase induced by hardening. Hardening to cold did not appreciably alter the relative osmotic relationship of fungus and host.

Infection of oats, barley, wheat, and corn with appropriate smuts did not change the degree of susceptibility to specific rusts.

Evidence is presented that suggests that resistance of Hope wheat in the mature plant stage may be partly determined by lack of availability of water to the parasites. This may also explain regional differences in susceptibility. These are tentative conclusions only.

Vital histological examination of the development of resistant flecks on Vernal wheat demonstrates that host cells are killed prior to the occurrence of any discernible injury to fungus organs.

A suggestion is made relative to the cause of the different degrees of permeability change associated with different rust reactions.

Present knowledge of the factors governing resistance of cereals to rusts indicates that, commonly, the property of resistance is specifically determined by inherent qualities of the host protoplasm. Resistance is a dynamic phenomenon expressing a resultant effect of the interaction between vital activities of host and parasite. The precise nature of these interacting factors and the physiological mechanisms involved are not understood. Among the rusts, it is improbable that any one factor exclusively determines resistance. However, it is possible that any one of the essential vital phenomena active in the micro-environment of the antibiotic cells may approach a critical state and become limiting to successful parasitism. Under such particular conditions,

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that phenomenon may be the one chiefly active in determining resistance or susceptibility. For the full understanding of resistance it is desirable that these critical phenomena be determined. A basic requisite for successful parasitism obviously is that an adequate supply of suitable nutrients be available to the parasite. If the host tissues contain nutrients of the type required by a particular parasite these nutrients must still be rendered available to the parasite. The rusts presumably derive their nutrients either from the vacuolar contents, or direct from the host protoplasm, if the general observation be true that these fungi exercise no hydrolytic action upon cell wall materials. In either instance some relatively non-injurious mechanism for the removal of nutrients is required, which, according to modern concepts of the living protoplast, involves overcoming the normal semi-permeability of the plasma membrane.

Permeability studies made by the writer (19, 20, 21, 22) have shown that with the various rusts examined an increase in permeability of the plasma membrane of cells in the vicinity of the parasitizing mycelium is constantly associated with susceptibility. This fact, coupled with the observation that the cells of the parasites have a higher osmotic value than the cells of their hosts, formed the basis of an hypothesis elaborated by the writer (20) to explain nutrient uptake by rusts. Resistance of Mindum wheat to *Puccinia graminis Tritici* Erikss. and Henn. race 21 was found to be associated with a greatly decreased solute permeability. This change would restrict availability of solutes to the fungus, both quantitatively and qualitatively. Treatment with chloroform vapour caused an increase in solute permeability and at the same time rendered Mindum less resistant to race 21. These results together with the conjecture outlined above tend to indicate a highly significant role for permeability change in the parasitism of the rusts and give some insight into at least one of the factors possibly active in determining "protoplasmic resistance".

The experiments reported below were designed to test these contentions and to obtain data on cognate interactions of the rust fungi and their hosts by investigation of widely observed rust phenomena, by the use of vital techniques in so far as possible.

Experiment I

AN INVESTIGATION OF THE BROWNING REACTION OF KUBANKA WHEAT TO CERTAIN RACES OF *Puccinia graminis Tritici*

The browning reaction is a peculiar reaction shown by a number of wheat varieties to certain races of *Puccinia graminis Tritici*. "Browning" occurs only at high temperatures (80 to 85° F.) and is manifest by the development of dark brown areas surrounding and extending some distance beyond uredinial sori. The reaction becomes evident shortly after the sori, at first typical of a susceptible host, have become erumpent. During the period of this colour change of normally green tissue to brown, urediniospore production is curtailed and finally ceases. Frequently, a small cluster of teliospores ultimately

marks each centre of infection. Photographs of Thatcher wheat showing various degrees of browning are shown in Fig. 1A.

Hart and Allison (6) have shown that the browning described above is at least partly due to the encystment of many of the rust haustoria. These organs become partly or completely enveloped in a cell-wall-like deposit of varying thickness, usually brown in colour. Hart and Allison state that these atypical structures may represent attempts at spore formation.

This abnormal reaction is evidently an indication that the micro-environment of the rust thallus has become unfavourable to further rust development, so that the host, which at first responds in a typical, susceptible manner, later shows a type of resistance. A study of the factors inducing this change is desirable as a contribution to our knowledge of the cause of disease resistance, and provides an opportunity to make further tests of the significance of permeability changes in the peculiar host-parasite relations of the rusts.

Accordingly, concomitant studies of the histopathological development and of permeability changes were made at daily intervals beginning as soon as sori were evident and continuing until inhibition of sporulation and extreme browning had occurred.

Seedling leaves of Kubanka wheat were inoculated with *Puccinia graminis Tritici*, race 34. One set of plants was held at 85° F.; another at 60° F. Part of the material was sectioned freehand at the appropriate stages of development and examined immediately: some without staining treatment, some after staining with vital neutral red. Other material was fixed, embedded in paraffin, and treated as described later. Part of the living preparations were used for determination of permeability to urea by the plasmolytic method as described in a previous publication (20). Comparative measurements were made of the permeability of cells of infected areas and of healthy areas of the same leaves.

To determine whether the material enveloping the haustoria was of fungus or host origin, tests for the presence of cellulose and of chitin were applied to fixed material by methods essentially those described by Rawlins (14). Other sections were stained with thionin-orange-G.

Pustules were first clearly visible eight days after inoculation. At this time no definite browning was externally visible, though the extent of the thallus was indicated by slight chlorosis. Sections revealed a particularly profuse development of mycelium. Haustoria were present in practically every parenchyma cell of the invaded region. Most of them appeared normal and characteristic of the species. Some, however, were partly enveloped in laminate aggregations of cell-wall-like material, most conspicuously disposed around the haustorial penetration thread or the base of the expanded part of the organ. At this stage colour discernment was questionable. Host protoplasts were living; chloroplasts present; cytoplasm apparently normal, behaving like that of healthy protoplasts in plasmolysis; vacuoles stained normally with neutral red though they appeared somewhat more turgid

than did vacuoles of uninfected cells. In general, except for the early stages of haustorial encystment, the infected tissues seemed typical of other susceptible wheat varieties at the same stage of development.

Permeability measurements made at this time indicated an increase in the solute permeability of infected cells in accord with that already found in other associations of various races of *Puccinia graminis* Pers. with susceptible varieties. This pronounced increase over the permeability of healthy cells is clearly depicted by the graph in Fig. 4C.

On the following day, nine days after inoculation, a suggestion of a brown tinge was apparent in the infected area around the sorus, being more definite towards the centre. Microscopical examination revealed that the deposition of wall-like material about the haustoria was progressing rapidly. Greater numbers of haustoria were affected; some haustoria were completely enveloped and showed a light brown coloration in the material first deposited. Protoplasts of haustoria and host cells were still living. Permeability of infected cells was still further increased as compared with the change evident on the first day of measurement.

During the next four days the fungus sporulated profusely, but the infected area of the leaf became progressively browner until the pale chocolate colour was quite conspicuous. Degeneration of chloroplasts was evident in cells near the sorus. Haustoria in most instances had assumed a chlamydospore-like form. The original haustorial walls (each about the same thickness as that of a young hypha) could be discerned with careful illumination but upon them had been deposited completely enveloping, thick, brown "pigmented" sheaths, the thickness of these sheaths sometimes exceeding one-third the diameter of a mature rust hypha. In each case this thickening formed a cylinder about the fine thread on which the expanded portion of the haustorium is borne, and ended at the inner surface of the cell wall of the host. Haustorium mother cells were never affected. Frequently, the presence of pores in the wall, such as occur in urediniospores, was apparent. All the above features are demonstrated in Fig. 1B. The shape of these chlamydospore-like organs varied. Sometimes the outline would be fairly regular, following the contours of the original haustorium. They might be spherical as in Fig. 1E, or elongate as in 1C. Frequently walls were echinulate giving these structures an appearance strongly suggestive of urediniospores. In later stages these structures sometimes assumed very irregular, bizarre shapes such as those shown in Fig. 1D. Occasionally, a decided suggestion of septation was apparent. Fig. 1G shows three closely grouped encysted haustoria very much resembling *Puccinia* teliospores in their general form. When terminal cells of hyphae could be found, more usually in substomatal cavities, these were commonly expanded and sometimes showed a tendency for abortive branching to occur. The profuse development of hyphae which occurs prior to browning should be noted in Fig. 1F. The same figure also shows the common occurrence of encysted haustoria.

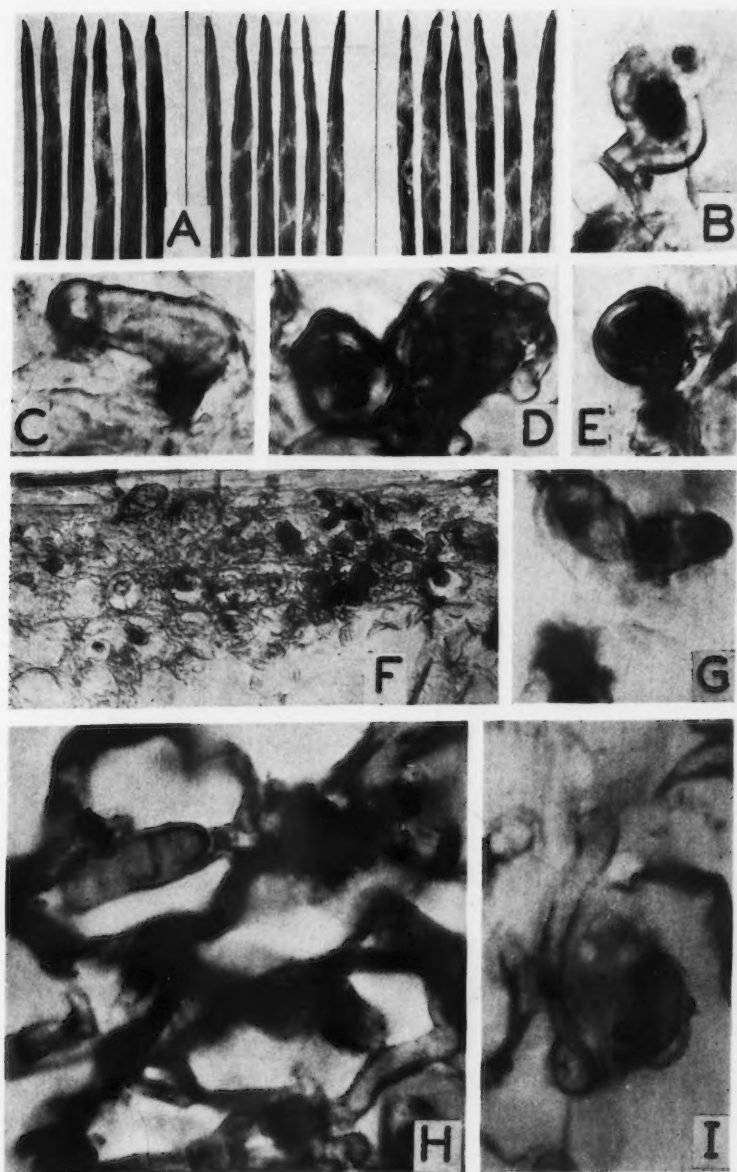


FIG. 1. A. Three degrees of "browning" induced at different temperatures on Thatcher wheat by *P. graminis* Tritic, race 34. (Material prepared by Dr. Helen Hart and shown through the courtesy of the Minnesota Agricultural Experiment Station.) B. C. D. E. F. Encysted haustoria of race 34 in Kubanka wheat; B and E—living (note neutral red stained vacuoles), $\times 1000$; C and D—protoplasts dead 17 days after inoculation (note irregular shape and knob-like projections in D), $\times 1200$ and 1500 , respectively; F—cross section of Kubanka leaf showing "browning" (note frequency of encysted haustoria and luxurious development of hyphae), $\times 80$. G. Three encysted haustoria, all apparently septate. H. Section of Kubanka wheat with an encysted haustorium after treatment with iodine-potassium-iodide-sulphuric acid as a cellulose test (note similarity of staining of encysted haustoria and hyphal cell walls, both being clearly differentiated from the host cell walls), $\times 1000$. I. A figure similar to H after the drastic test (potassium hydroxide, iodine-potassium-iodide, sulphuric acid) for chitin. The dark staining haustorial and hyphal walls is a positive indication of chitin, $\times 1000$.

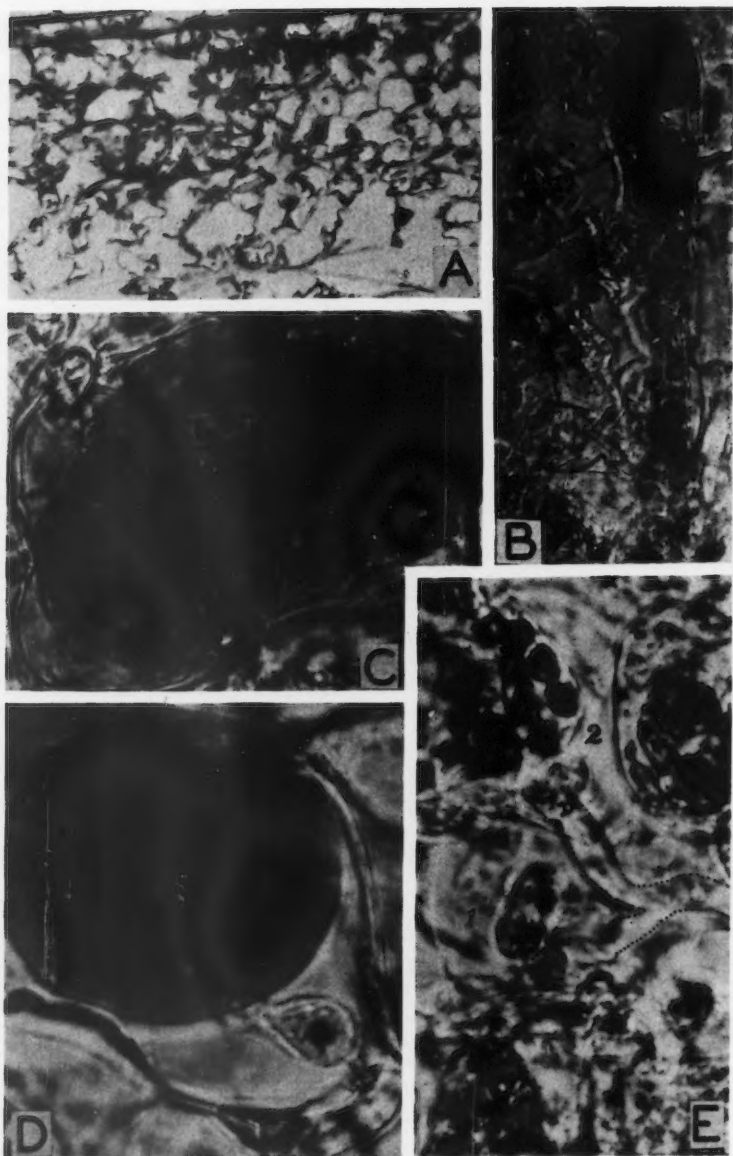


FIG. 2. A. Section of Kubanka leaf in early stages of "browning" after cellulose test with iodine-potassium-iodide-sulphuric-acid, haustorial sheaths and hyphal walls are both clearly differentiated from host cell walls, indicating fungus origin of the sheaths. B. A vitally stained section through a young "fleck" on Vernal wheat caused by *P. graminis* *Tritici* race 34 (note living rust hyphae traversing a zone of dead host cells, while a cell at the edge of this zone and about to receive a haustorium is still alive and apparently normal in every way), $\times 400$. C and D. Cells from rusted wheat leaves plasmolysed in calcium chloride solution, indicating the extracellular nature of the haustoria, $\times 1200$. E. Vital preparation of cells of Vernal wheat in the region of a young "fleck" caused by race 34 (note mature, living haustorium in dead cell at 1 while the contiguous cell at 2 is normal though having a haustorium mother cell appressed against it (1 and 2 in different focal planes; hence poor focus)), $\times 1200$.

Up to this time, the modified haustoria were found only in living cells as established by neutral red staining and by plasmolysis tests. Similar tests demonstrated that the haustoria themselves were also living. The dark central regions of the photomicrographs in Fig. 1, B and D, are vitally stained vacuoles. Their outlines tend to be indistinct because of the difficulty of photographing through a thick, dark, amorphous layer at high magnification.

As stated by Hart and Allison (6), the brown appearance of the lesions is partly due to the profuse distribution of these coloured abnormalities, but sections of living tissue show that the host cell walls are also browned to a considerable extent, and vacuoles seem to contain greater quantities of visible amorphous particles. Clusters of small, brownish, seemingly translucent, oil-droplet-like particles, sometimes resembling in configuration small, floating colonies of *Staphylococcus* cells and displaying Brownian motion, are common in the host vacuoles. The possibility was considered that some of these aggregations and the material causing wall discoloration were, perhaps, the substances referred to frequently as "tannic" compounds. Tests as used by Dufrenoy* indicated that this was not the case. Instead, tests with Sudan IV positively demonstrated the fat-like nature of the globular particles. Beauverie (2) describes similar bodies being formed as a result of disruption of chloroplasts by extreme changes in hydrophily. Small amounts of amorphous deposits on walls of dead cells were found to give a positive reaction for tannins using 10% ferric chloride as reagent.

During this period, and up to the seventh day after pustule formation, the solute permeability of infected cells showed progressive increase as is indicated in the graph shown in Fig. 4C. On the seventh day several infected host protoplasts were dead, while a high proportion appeared to be in unhealthy condition as indicated by their inability to withstand plasmolysis for more than a short time; by partial loss of chlorophyll from chloroplasts and by the presence of granular, faintly brownish plastids disorganized to the extent of showing no evidence of a continuous bounding membrane. At this time permeability values were of the same order as of the immediately previous determinations, but were somewhat erratic. Host tissues contained much inter- and intracellular amorphous material, probably degradation products of killed cells.

Plants at this stage were then placed in a greenhouse maintained approximately at 60° F., in order to see whether this treatment would induce the "chlamydospores" to germinate. In four to five days, the browned lesions became partly or completely encircled by uredinial sori and the newly invaded areas beyond the necrotic region showed no further manifestation of resistance, indicating that at least some part of the rust thallus had remained viable and that the factors responsible for development of "resistance" at high temperatures had ceased to function on removal of the plants to lower temperatures. Microscopical examination at this time revealed the fact that new fungal

* Forwarded to the writer through personal correspondence.

growth had occurred by elongation of existing hyphae, and that in no instance had the encysted haustoria shown signs of germination. Many of these abnormal structures were examined, but all were dead. Neutral red failed to indicate the presence of vacuoles such as were easily detected in urediniospores attached to these same sections. Figs. 1C and 1D are of the dead fungus organs, in which the absence of vacuoles as determined by neutral red is clearly apparent. Instead, collapsed remnants of the original haustorial protoplast and small amorphous aggregations of unknown material may be seen in the lumen of the haustorium. Similar examinations were later made on two other occasions, with essentially the same results in each instance.

The microchemical tests made to determine whether the haustorium-enveloping material was of host or fungal origin indicated clearly that the latter was the case. Figs. 1H and 2A are photographs of the same preparation at different magnifications after the iodine-potassium-iodide-sulphuric-acid test for cellulose had been applied. Host cell walls give a strongly positive test (a pronounced blue colour) while the ensheathed haustoria react precisely as do the intercellular hyphae, both being negative except for possible indications of traces of cellulose. The colour differences are clearly rendered in these last two photographs. Fig. 1I is a photograph of the remnant of a section that has undergone the drastic treatment for detection of chitin. By the method (potassium hydroxide, iodine-potassium-iodide, sulphuric acid) described by Rawlins (14), chitin is determined by development of a purplish colour reaction. An attempt to demonstrate the differential colouring observed between host cell remnants and the haustorial sheath material in a positive chitin reaction is made in Fig. 1I. The hyphae and the material deposited about the haustoria were similarly stained and clearly distinguished from the yellowish colour of the host residuum.

Conclusions

The results reported above offer good evidence that the browning phenomenon, as observed on Kubanka wheat infected with *Puccinia graminis Triticis*, race 34, is an expression of a change in the micro-environment of the fungus induced essentially by high temperature which so modifies the interaction between host and parasite that the host reaction changes from complete susceptibility to a type of resistance leading to a cessation of fungal growth. That the observed change in reaction might be caused by a belated development of hypersensitivity of host tissues would not appear to be true since the encystment of haustoria occurs only in living cells. The pronounced permeability increase of infected cells, which is progressive up to the time of death of the cells, may be significant and an hypothesis to explain the change from susceptibility to resistance is tentatively offered. The fungus induces a permeability increase in host cells characteristic of a susceptible reaction (20) as measured at room temperature (70° F.). However, Levitt and Scarth (11) have demonstrated that permeability has a high Q_{10} over the range of temperatures under consideration, so that at the higher levels permeability increase

may be considerably augmented. On the basis of earlier reasoning (20) this would lead to a relatively rapid availability of solutes to the fungus, which would facilitate speedy and luxurious vegetative growth. An incubation period four days shorter at 85° F. than at 60°, a dense hyphal development at 85°, and the profuse initial sporulation are in accord with this suggestion. However, with rapid production of mycelium and the presence of a large thallus, the supposed membrane-modifying secretions of the rust would presumably be produced more copiously, so that progressive permeability increase from this cause could be expected. In the meantime, host cells are being heavily taxed for those solutes to which permeability has been increased and which may be assimilated by the fungus. Under extreme conditions of increased permeability and nutrient withdrawal, metabolic derangement would be expected with consequent interference in the delicate rust relationship, partly by formation of substances toxic to the fungus, of which there were definite indications, and partly due to the combined effects of depletion and modification of food supply. The degree to which each factor may be effective can not yet be postulated. The rapid formation of a protective covering about the haustoria might be interpreted as a response to either a toxic environment or to lack of food. Death of the host cells might be due to exhaustion of specific materials used by the rusts, to a lethal permeability change, or to some factor of injury of which permeability change may be an effect.

Experiment II

AN INVESTIGATION OF PERMEABILITY CHANGES ASSOCIATED WITH THE MESOTHETIC (α) REACTION OF *Puccinia graminis Triticis* RACE 56 ON THATCHER WHEAT

The mesothetic or α reaction, as implied in stem rust of wheat, signifies the development of a range of reactions, sometimes from complete susceptibility to pronounced resistance, occurring on a single leaf of certain wheat varieties when inoculated with urediniospores of a single rust race (17). This can not be explained on the basis of the presence of a number of biotypes in a given race since spores from any single sorus, of monosporous origin, whether of a type indicating resistance or susceptibility, will again provide a similar range of reactions.

Hence, it would seem that in the varieties that manifest the α reaction, a particularly delicate balance exists between the interactive factors of host and fungus, and that any slight local change in the micro-environment of a particular thallus would tend to modify the reaction. Hart has shown that temperature and light intensity influence this reaction range and an α reaction may be converted into a homogeneous demonstration of susceptibility under certain environmental conditions (unpublished data). Examination of the α reaction presents an opportunity to study extremes of susceptibility and resistance with all cells of the parasite and all cells of the host, so far as is known, respectively genotypically identical. It is difficult for the author to visualize such an immense number of somatic mutations occurring in a

single leaf as would be required to explain the variation in susceptibility on genetic differences. If permeability increase can be associated with susceptibility on the one hand, and permeability decrease with resistance on the other, in material such as this, then evidence will be available which seems strongly in support of that already presented by the author (20, 22) concerning the importance of degree of permeability change in determining susceptibility and resistance.

Accordingly, seedling leaves of Thatcher wheat were inoculated with *Puccinia graminis Tritici*, race 56 and grown at temperatures approximating 60° F., 70° F., and 85° F. Length of incubation period varied inversely as the temperature. Infections on the plants grown at 85° F. showed the greater tendency to produce type 4 reactions (highly susceptible), and flecks without minute sori were rare. The greatest proportion of flecking (extreme resistance) was evident at 60° F. though definite type 4 pustules were also present. About five days after pustule formation the type 4 reactions at 85° and to a lesser extent at 70° F. were modified by development of a necrotic ring around a green island of leaf tissue bearing the central sorus.

After the sori were well developed, measurements were made of the permeability to urea of cells (*a*) in the tissue invaded by the mycelium surrounding type 4 pustules, (*b*) from flecks, and (*c*) from healthy tissue of the same leaves all being from plants grown at 60° F. Sectioning of the flecks required care. The method adopted was to cut out a leaf fragment on which a fleck was centred. The dimensions of these pieces of tissue would mostly be from 1 to 3 mm. A number of these (up to 10) were then arranged in parallel fashion in a cleft piece of boiled pith and sectioned longitudinally by rapid strokes with a sharp razor. Suitable sections were then sorted out from a dish of tap water containing vital neutral red into which all the accumulations of the wet razor had been brushed. Permeability determination was made by the method already described.

Sections of the flecks revealed a relatively dense development of mycelium ramifying amongst practically all the discoloured tissues of the fleck. The amount was considerably greater than that observed in flecks of Mindum wheat inoculated with race 36. In some instances subepidermal stromatic mycelial aggregations indicated abortive attempts at pustule formation. A tendency to form encysted haustoria is fairly common though much less so than in the reactions described on Kubanka. During the early stages of fleck discernment a large proportion of living cells were present in the etiolated zone. Within a period of three days after appearance of the fleck all cells in this region were dead. Aggregations of small, brown, globule-like particles similar to those described in Kubanka are present intercellularly and in senescent cells. Even before death a suggestion of a brownish discoloration of host cell walls is apparent in unstained sections. The mycelium remains alive at least for several days after death of most of the affected host cells, though the hyphae are seen to contain many large vacuoles, and their cytoplasm is more translucent than that of normally active fungal cells.

Thus, an active mycelial development occurs for some time after infection, and then a factor tending to make conditions unfavourable for further mycelial growth intervenes. The origin of this factor is not known, but it seems to be most acutely effective against the host since infected host cells die some time before the adjacent mycelium. A similar trend of events may explain the development of the necrotic zone some distance from a type 4 pustule as already described, so that a reaction originally of type 4 later is suggestive of a type 2 reaction. A time factor seems to be operative in conjunction with other factors determining degree of susceptibility in this instance.

Permeability measurements were first made with those few living cells present in the young flecks. Compared with healthy cells, these were found to have an irregularly increased permeability to urea. This was probably an additional indication of senescence. Permeability studies were then made of cells, among which mycelium was dispersed, at the border of the discoloured flecks; of cells interspersed with mycelium associated with type 4 pustules; and of cells in uninfected tissue of the same leaves. The graph in Fig. 4A clearly shows the difference in permeability between these three regions. The curves were prepared by plotting the percentage number of cells deplasmolysed at stated time intervals after having been initially plasmolysed to the same degree. In order to extend the number of determinations possible with a particular lot of material, the cells were plasmolysed in a solution three times more concentrated than an isotonic solution. Preliminary tests indicated no practical objection to use of this rather high concentration. An attempt was made to establish each point on the curve by an examination of approximately 100 cells. This was not always possible with tissue from flecks. Details of the determinations made are available in Table I. It is evident that the living host cells at the border of a fleck have a very greatly decreased permeability as was found associated with resistance to form 36 in Mindum wheat, and that cells associated with a susceptible reaction demonstrate

TABLE I

PERMEABILITY TO UREA OF TISSUES OF THATCHER WHEAT GIVING DIVERSE REACTIONS TO *Puccinia graminis Tritici*, RACE 56 (x REACTION)

Flecks			Type 4 pustules			Healthy tissue		
Deplas. time (min.)	Cells deplas., %	No. of cells observed	Deplas. time (min.)	Cells deplas., %	No. of cells observed	Deplas. time (min.)	Cells deplas., %	No. of cells observed
45	0	100	35	21	95	35	25	90
75	16	60	45	42	47	50	30	85
90	20	25	50	85	93	60	31	63
100	20	40	70	89	87	95	46	83
105	22	57				95	43	151
110	22	72				100	46	102
110	23	68				130	87	138
120	25	74						

an increased permeability. This is in accord with susceptibility reactions with several races and different wheat varieties. That these changes in the several instances determined are merely chance coincidences does not seem likely.

Experiment III

THE EFFECT OF HARDENING TO COLD ON RUST REACTION

The previous studies by the author (already referred to) and the foregoing experiments indicate that susceptibility to rust is, in all instances studied, associated with increase in cell permeability. Scarth and co-workers (10, 15, 16) have shown that the process of hardening plants to cold also induces an increase in permeability. Hence, if permeability increase is an essential prerequisite to successful parasitism by a rust fungus, then cold-hardened plants might be expected to offer a more congenial substrate to those races that do not normally develop very vigorously on a particular host, *provided* that the effect of hardening and maintenance of the hardened condition does not influence other factors to the detriment of the parasite.

Two wheat varieties, Marquis and Kota, known to permit a certain range in reaction with race 38 were used in this experiment. The plants were divided into four groups of six pots of each variety, each pot containing about 12 seedling plants. Series *A* was hardened before inoculation by placing in a lighted cold chamber at 2° C. for eight days. They were then inoculated, incubated in a moist chamber for 36 hr., then kept at 70° F. during the day and at 2° C. at night, the latter precaution being to maintain hardness. Series *B*, really a check on the effect of the diurnal temperature fluctuation, was inoculated without hardening and then kept at 70° F. during the day and 2° C. at night. Series *C* was inoculated before hardening, and after the two day incubation period was hardened for eight days in the 2° chamber, after which it was subject to the same day and night temperature alternations. Series *D*, a check, was inoculated without cold-chamber treatment at all and was kept at 70° F. The experiment was repeated three times, though, since the diurnal temperature fluctuation was found to have little effect it was ignored in the last two attempts. In addition, on two occasions after formation of pustules in Series *B* (no continued hardening period) half of the Marquis plants were placed for eight days in the hardening chamber, and the reactions compared with those of the unhardened members of this group. The reactions of the hardened plants were slightly more pronounced than those of the others, i.e., the extent of thallus and diameter of sorus were greater. A somewhat more vigorous development of rust is thus evident as a result of hardening at this stage even though the unhardened series were at optimum temperature.

The pustules that developed on hardened plants, whether inoculated before or after hardening, were of essentially the same reaction type as those appearing on plants grown continuously at 70° F. Marquis characteristically gives a type 2 reaction with race 38, i.e., a small sorus centred in a green island sur-

rounded by a zone of necrotic tissue. However, in general, where hardening occurred before pustule formation, the sori of the hardened plants were smaller than of check plants, but the margins of the lesions were demarked by mildly etiolated zones rather than by strongly chlorotic and necrotic peripheral zones typical of lesions on the unhardened plants. These differences are indicated in Fig. 3, D and C, respectively.

The possibility that increased osmotic pressure commonly associated with hardening to cold might reduce availability of water to the parasite and so restrict its development was investigated. Hardened leaves did indicate an increase in osmotic pressure, but never to the extent of being equal to or greater than that of the fungus (see Table II).

TABLE II
THE EFFECT OF HARDENING TO LOW TEMPERATURES ON OSMOTIC PRESSURES
OF MARQUIS WHEAT AND *Puccinia graminis* *Tritici*, RACE 38

Osmotic pressure in atmospheres			
Unhardened		Hardened	
Wheat	Rust haustoria	Wheat	Rust haustoria
12.06 13.65 13.20	18 - 20	14.27 17.65 16.39	18.4 - 21.6

The author is of the opinion that any initial effect of the increased permeability induced by hardening tends to be obscured by the effects of other factors. First, the seedling leaves of unhardened plants are about 15 days old at the appearance of pustules, while hardened plants are at least twice that age at the same stage of pustule development. Commonly, other leaves must be cut back in order to prevent senescent degeneration of the inoculated leaves. Secondly the effects of hardening, other than of permeability change, that may exert some effect on the predisposition of wheat to rust are not known. Also, it is probable that any rust thallus that can become successfully established in the tissues of its host has the ability to cause permeability change by its own mechanisms and so quickly becomes independent of the permeability change caused by hardening. The extreme specificity demonstrated in the relationship between wheat varieties and rust races is not easily offset.

Experiment IV

THE EFFECT OF SMUT INFECTION ON SUSCEPTIBILITY TO RUST

The papers of Hart (5), Welsh (24), and Straib (18) refer to many workers who have stated that various cereal plants when infected by smut appeared more susceptible to rusts. Direct investigation of this relationship seems to have been limited in extent, except for the recent work of Straib (18) who

found that wheat varieties of a group having an unstable type of resistance during the mature plant stage did show an increase in susceptibility to certain races of *Puccinia glumarum* as a result of infection with *Tilletia tritici*. Plants in the younger stages of development or which normally possessed a stable type of resistance showed no such response. The degree of susceptibility of susceptible varieties was not changed by smut infection.

The writer began this study without having read Straib's report so that no consideration was given to his different categories of resistance. However, hosts and rust races were chosen to provide several expressions of resistance, and the effect of the presence of smut upon the development of rust on both maturing and seedling hosts was observed. Permeability determinations of tissues from smutted and non-smutted plants were intended if significant changes in rust reaction became manifest.

Common varieties of oats, barley, wheat, and corn were infected with their respective smuts, *Ustilago levis*, *U. hordei*, *Tilletia levis*, and *U. zeae*. Oats and barley were grown until mature smut masses were evident and then inoculated with *Puccinia graminis avenae* Erikss. and Henn. and *Puccinia graminis secalis* Erikss. and Henn., respectively. A single but unknown race of rust was used in each instance. The smutted corn and wheat plants were inoculated while young with their respective rusts, *Puccinia sorghi* and *P. graminis Tritici*. Two wheat varieties were used: one, Thatcher, being relatively resistant; and the other, Ceres, being susceptible to the particular strain of smut used. Thatcher was inoculated with race 56 which normally gives an x reaction, and Ceres with 38 and 19 which usually develop a very low type III reaction on this host. To inoculate with smut, wheat kernels were heavily contaminated with smut chlamydospores and grown in flats for two weeks at 10° C. before potting at the rate of about 20 seedlings per pot. They were then grown in a greenhouse at a temperature mostly ranging from 70° to 80° F. Uninoculated seed to provide check plants was treated similarly. This method of inoculation with these particular varieties has given a very high proportion of smut infection in previous years*.

Because of the heterozygous nature of corn, which gave a considerable range of susceptibility, comparison, in this instance, was made between the rust development on smutted and non-smutted leaves of the same plants, local smut lesions having been induced by hypodermic injection of a mixed suspension of sporidia of two compatible strains of *Ustilago zeae*.

The entire experiment provided no evidence that smut caused modification of susceptibility to rust, with the exception that rust sori on oats and corn became erumpent on smutted plants from one to two days earlier than on non-smutted plants. The lack of effect, once the sori were mature, is indicated in Fig. 3, G and H. This slight "stimulation" on corn was localized, being confined to sori developing within 2 to 3 cm. from the margin of a smut lesion. Normal sori appeared within 1 to 2 mm. from the margin of a smut gall.

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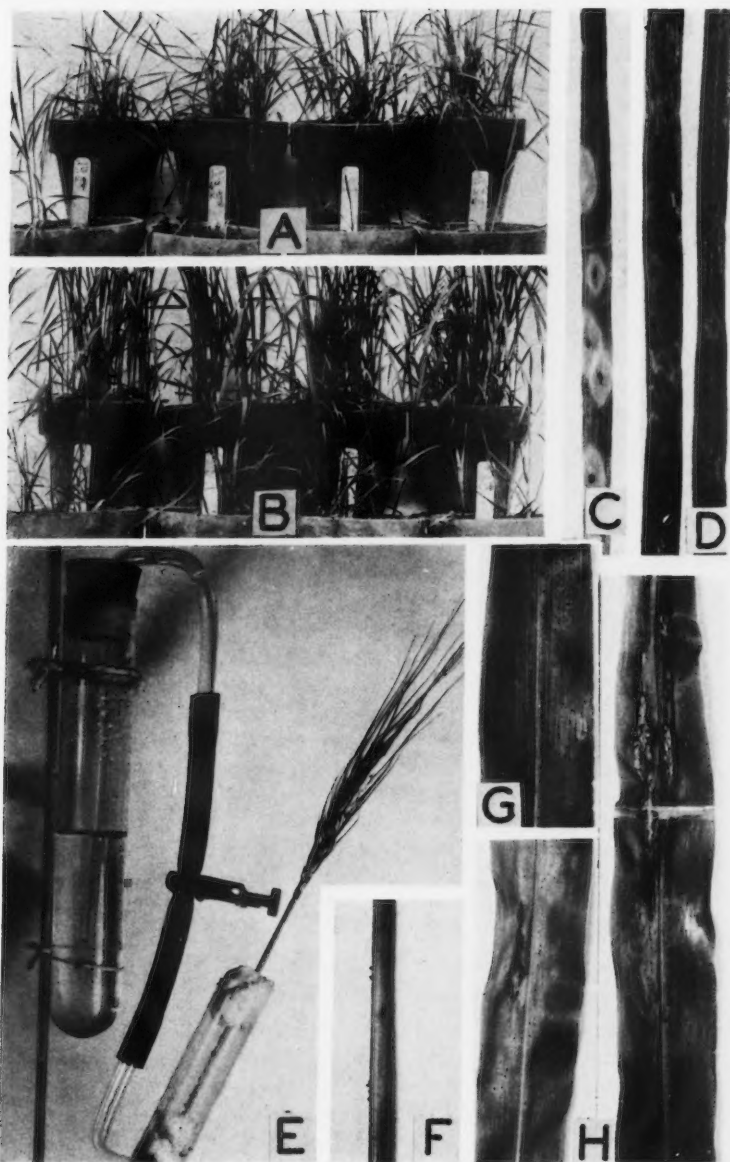
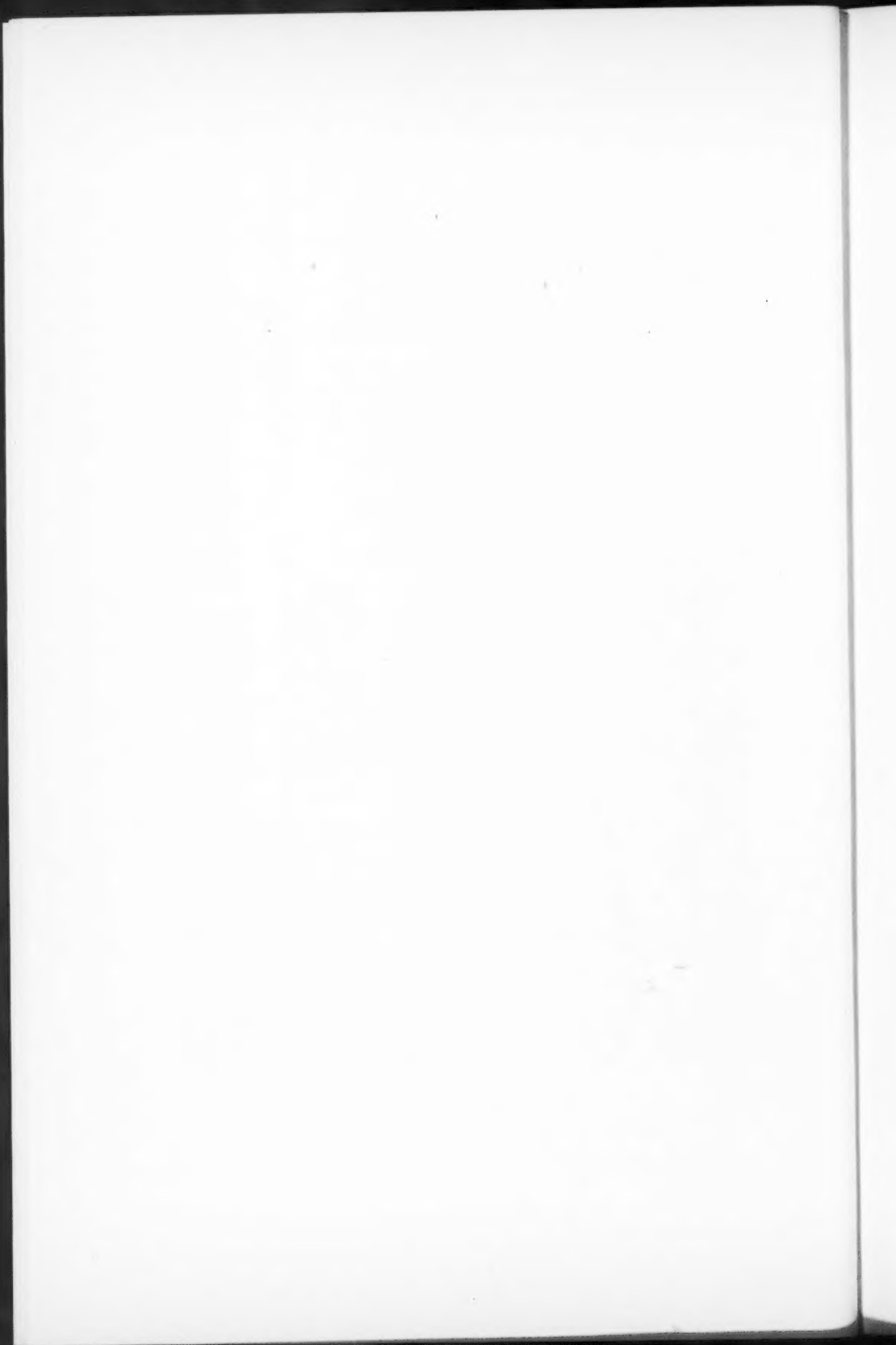


FIG. 3. A and B. The effect of bunt on root rot caused by *R. Solani*, upper rows of pots not bunted, lower rows bunted; A—Ceres, B—Thatcher. C and D. Pustules formed by *P. graminis* Triticum, race 38 on Marquis wheat: C—after the plants had been hardened to cold, D—normal wheat; notice greater amount of bordering necrosis in the normal as compared with hardened wheat. E. The apparatus used to maintain an atmosphere saturated with water about the region of a Hope peduncle which is normally highly resistant, $\times \frac{1}{2}$. F. Pustules on the peduncle shown in E after 15 days incubation (note absence of necrosis and vigorous spore formation even though the sori are small), $\times 2$. G and H. Golden Bantam corn with pustules of *P. sorghi*: G—free from smut, H—infected with *Ustilago zeae* (note lack of effect of smut on rust).



No modification of rust whatever was noted on mature smutted barley or young wheat. A résumé of this experiment is presented in Table III.

Measurements of the effect of smuts on the permeability values of their host cells have not yet been made.

TABLE III

THE EFFECT OF SMUT INFECTION ON THE DEVELOPMENT OF VARIOUS CEREAL RUSTS

Host plant		Pathogen		
Variety	Stage of development	Smut	Rust	Effect of smut on rust
Oats-Anthony	Maturing	<i>U. levis</i>	<i>P. graminis avenae</i>	No change in reaction; sori erupt one to two days earlier
Barley	Maturing	<i>U. hordei</i>	<i>P. graminis secalis</i>	None
Wheat-Thatcher	Seedling	<i>T. levis</i>	<i>P. graminis Tritici</i> , race 56	None
Wheat-Ceres	Seedling	<i>T. levis</i>	<i>P. graminis Tritici</i> , race 19	None
Corn-Golden Bantam	Young	<i>U. zeae</i>	<i>P. sorghi</i>	No change in reaction; sori erupt about one day earlier

By chance contamination with a root rotting organism (*Rhizoctonia* was isolated) a decided difference was made apparent between the susceptibility of smutted and non-smutted wheats to root rot. Smutted and non-smutted plants were handled precisely in the same manner throughout, even to incubation in the same chambers after inoculating with rust spores. From eight pots of bunt-inoculated Thatcher wheat a total of 37 plants were living 20 days after rust inoculation, compared with a total of 144 plants in eight pots of non-bunted specimens. Ceres showed the same effect, being even more susceptible; 29 bunted plants surviving from 10 pots; 113 non-bunted plants surviving from seven pots. The extreme difference in susceptibility is indicated in Fig. 3, A and B.

Experiment V

AN INVESTIGATION OF THE MATURE PLANT RESISTANCE OF HOPE WHEAT TO *Puccinia graminis Tritici*

Hope wheat has been considered a variety of great potential value to plant breeders because it possesses resistance to many races of *Puccinia graminis Tritici* during the latter phases of its growth. It is highly resistant during its more mature stages of development to certain rust races to which it is susceptible during the seedling stage. Other varieties with this property have been determined by Goulden *et al.* (4). *Puccinia graminis Tritici*, race 21 develops type 4 pustules on seedling Hope, but only necrotic flecks or small type I pustules bordered by a sharply demarked necrotic zone on plants at or beyond the "boot" stage. Hope demonstrates another apparent anomaly in that mature plants, normally resistant, will prove susceptible if inoculum of

a suitable race (e.g. 21) is injected hypodermically into the lower tissues of an internode, or if uredospores are introduced in any way between a leaf sheath and the culm (13). After experimental verification of these facts an experiment was planned to determine whether resistance and susceptibility at different stages of development of the host could be explained by degree of permeability change at the various stages.

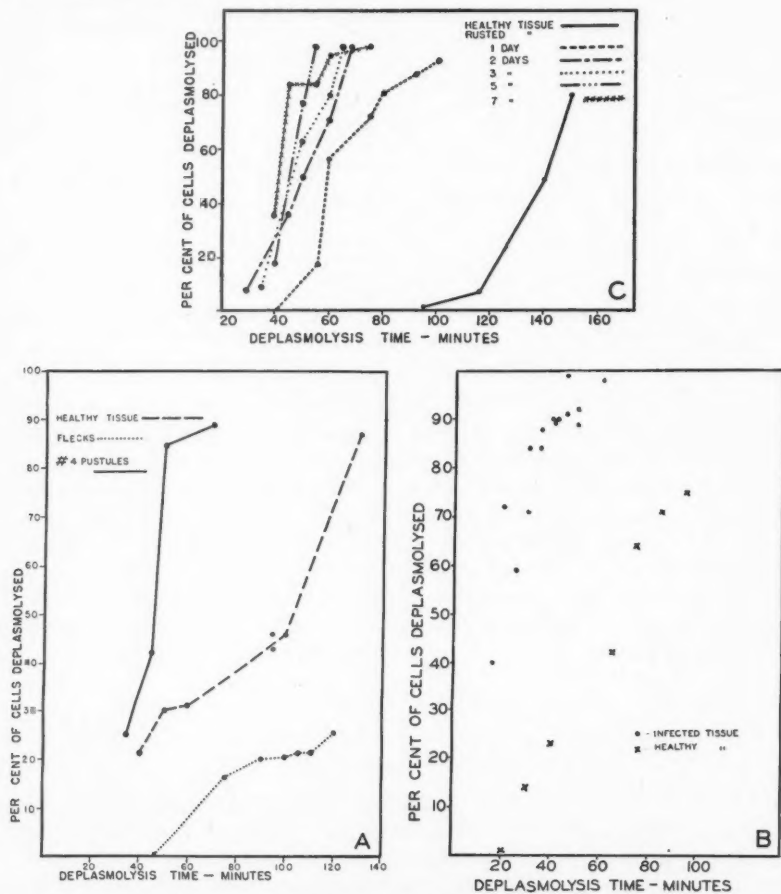


FIG. 4. Permeability to urea estimated by observing the percentage of cells deplasmolysed at stated time intervals after plasmolysing in a solution of twice isotonic strength. Each point on the curves represents observations of approximately 100 cells. A. Different degrees of permeability change in cells associated, respectively, with susceptible-(type 4) and resistant-type (flecks) infections of Thatcher wheat caused by *Puccinia graminis* Trilici, race 56, in a manifestation of the "x reaction". B. Permeability increase caused by *Puccinia graminis* Trilici, race 21, on seedling leaves of Hope wheat. C. Permeability changes associated with the "browning" reaction of Kubanka wheat to *Puccinia graminis* Trilici, race 34. Permeability measured on successive days after pustule formation.

Using urea as test substance, solute permeability was determined as already described. A pronounced increase in permeability was found to be associated with seedling susceptibility of Hope to race 21, just as has been found to be a common accompaniment to rust susceptibility wherever investigated. Fig. 4B clearly expresses this result, each point having been determined by observation of approximately 100 cells. It is unfortunate that illness prevented determination of an adequate number of mature plant permeability reactions from this same set of plants. In the one set of measurements obtained (from tissues bordering necrotic flecks on leaves in late stages of maturity) permeability was greater than that of healthy seedling tissue but less than that of susceptible rusted tissue. However, osmotic values as a prerequisite to permeability estimation were determined by the plasmolytic method, and in one set of plants the relative values for different organs of the plant seemed to bear a relation to their susceptibility. Seedling leaves were found to range in osmotic value from 11.0 to 11.82 atmospheres; leaves from mature plants 17.8 atmospheres; culms ($\frac{1}{2}$ to 1 in. above a node) 11.8 atmospheres; glumes 11.2 atmospheres. Seedling leaves are susceptible, leaves of mature plant, resistant; the portions of culms enclosed in a leaf sheath, susceptible; glumes, susceptible. This relationship was checked by using an entire set of newly made reagents and by observing sections of all tissues in a plasmolyte of the same concentration. In a 0.2 *M* calcium chloride solution (12.42 atmospheres) cells from mature leaves were turgid; from other tissues, plasmolysed. The osmotic value of intercellular hyphae in mature leaves was then measured as described in a previous publication (20) and found to be equivalent to ± 17.4 atmospheres. Such results, however, were not consistently obtained. Examination of another series of plants yielded results more in keeping with those of Johnson and Johnson (8) who found no correlation between osmotic pressure and resistance. The value for mature leaves in this second determination was 13.3 atmospheres—considerably less than that of the fungus (Table IV). The high values indicated in the first series

TABLE IV

THE OSMOTIC VALUES OF VARIOUS ORGANS OF HOPE WHEAT AT DIFFERENT STAGES OF DEVELOPMENT. DETERMINED BY THE PLASMOLYTIC METHOD

Osmotic pressure in atmospheres				
Seedling plants	Maturing plants			
Series I	Series I (droughted)			
	Leaf	Culm	Glumes	Rust hyphae
11.2 11.2 11.0	17.8	11.8	11.2	± 17.4
Series II	Series II (not droughted)			
11.8 11.4 11.8	13.25 13.34 13.28			18.0

may possibly be accounted for by the fact that during a period of indisposition on the part of the writer the plants received infrequent watering and are believed to have made metabolic modifications as a response to drought.

The second group of Hope plants examined gave the same expression of rust resistance as did the droughted plants and, even though high osmotic pressure *per se* did not seem to be indicated as a cause of resistance, the possibility still remains that lack of availability of water may be a contributing factor to resistance in this group. This thought was prompted by the observation that, since the younger parts of the plant have a lower osmotic pressure than the older, the water reaching them presumably flows in a direction opposed to that indicated by osmotic gradient. Johnson and Johnson (8) made a similar statement. Ursprung and Blum (23) and others referred to by Meyer (12) have demonstrated the common occurrence of such a relationship, and as a consequence, the need to recognize "suction pressure" or "diffusion pressure deficit" as the factor controlling water movement within plants has been recognized. Another factor that actively influences water flow in plants, is that referred to by Bennet-Clark *et al.* (3) as "secretion pressure".

The fact that those parts of the mature Hope plant that are susceptible to race 21 are also those that are best assured of a ready water supply stresses the possibility of the importance of this factor in influencing susceptibility. An experiment was therefore devised to maintain the most resistant part of the mature Hope plant in an environment saturated with water vapour, without having to subject the whole plant to an injurious environment, so that competition for water between host and parasite would be minimized. Accordingly, an apparatus such as is shown in Fig. 3E was prepared to provide an environment resembling as closely as possible that offered to a spore lodged between the leaf sheath and culm, which, as already indicated, induces a reaction of susceptible type. A small glass cylinder was placed around a peduncle of a potted plant leading to an inflorescence at some stage past flowering. The cylinder was secured about two or more inches above the flag leaf and loosely plugged with cotton wool at both ends. The lower plug was kept moist by a slow stream of water from a siphon arranged as shown in Fig. 3E. Water was added to the upper plug if at any time condensation droplets were not visible within the tube. The stem was lightly rubbed, wetted, and spores dusted on to the resulting film of water. No other incubation chamber was necessary. In view of the fact that Hart and Zaleski (7) have shown that low light intensities can render Hope susceptible, some cylinders were covered with black paper. No pustules developed on darkened peduncles, probably because of the occurrence of general chlorosis and necrosis. On the non-darkened stems the percentage of infection was low, but where infection did occur sori developed that were of susceptible type and quite devoid of any bordering necrosis. The sori that developed on the peduncle shown in Fig. 3E, and which are seen to be sporulating freely, were not accompanied by necrotic tissue (Fig. 3F). Pustules were smaller than

is typical for a vigorous type 4 pustule, but closely resembled those produced naturally from inoculum enveloped by a leaf sheath. Very high greenhouse temperatures prevailing during the incubation period of a duplicate series of plants led to the development of telial sori.

Histological Examination of Rusted Hope Wheat

Preparation of the many sections necessary for permeability determinations provided an opportunity to make a number of histological observations of some interest. A striking feature of the infected mature plant tissue showing resistance was the common distribution of aggregations of yellowish globules from sizes smaller than a micron to much larger sizes apparently resulting from coalescence of a number of the smaller globules. This was particularly true of mature leaf tissue. No such bodies were observed in leaves from seedling plants or in glumes. In addition, the spores that developed from resistant type pustules contained relatively large quantities of apparently the same yellowish material to a far greater extent than in any other uredospores observed by the writer. Often the nucleus was apparently enveloped in a sheath of this material, or about half the total volume within the exospore would be occupied by yellowish masses. No experiment was made to substantiate any particular significance of this material. It presumably was of oily nature because of its pronounced affinity for Sudan IV. A similar substance was described earlier in the discussion of "browning".

Indications that "mechanical resistance" such as described by Hart (5) was being operative and partially successful were frequently observed in mature leaves and peduncles. Evidence that the fungus found difficulty in rupturing the epidermis and cuticle while attempting to sporulate was clearly observed. The massed hyphae that form the normal pseudostromatic base for a sorus commonly appeared compressed and confined to a small area so that a structure suggestive of a sporodochium resulted. Several instances of initial sori that remained confined within the host tissues were also seen. However, it should be noted that the potential mechanical resistance in the glumes is much greater than in any other part of the plant as indicated by thickness of cuticle, of epidermal and hypodermal cell walls, and by the extreme resistance these tissues offer to a sectioning razor. Nevertheless, these tissues offer no evidence of repression of sorus formation, the entire glume sometimes appearing as a practically continuous sorus. This suggests that in Hope wheat mechanical resistance cannot prove effective unless some physiological expression of "protoplasmic resistance" has already reduced the vigour of the parasite, and prevented the fungus cells from developing sufficient turgor pressure to rupture mechanical barriers. This seems to strengthen the possibility already stated that relative availability of water may play some part in determining mature plant susceptibility in the instance considered.

The work of Johnson and Newton (9) published after completion of this study is also in keeping with this suggestion in that leaves and stems of shaded

Hope plants were both more susceptible and possessed a higher water content than non-shaded plants.

Another observation of particular interest in this consideration of resistance was a positive demonstration that a rust haustorium does not become intravacuolar, but merely invaginates the host cell membrane so that a continuous interface between host cytoplasm and haustorium persists. This is in agreement with the general consensus of opinion as previously outlined (20), though the writer had not felt the evidence presented to be very convincing, particularly after having studied fixed preparations that seemed to indicate otherwise. However, during the current study with vital preparations a number of haustoria were observed to be external to living host protoplasts. One such protoplast was strongly plasmolysed in 0.5 *M* calcium chloride and is shown in this condition in Fig. 2D. The protoplast became rounded and so reduced in volume that the haustorium was left free in the plasmolyte. It will be noted that the protoplast appears to have been pushed over to one side of the cell by the haustorium. If the haustorium had been intravacuolar the expanded portion of the haustorium would have held the protoplast against the cell wall next the point of entrance of the haustorium. Slightly lower concentrations of calcium chloride were then progressively drawn under the cover slip, and as the protoplast expanded the haustorium was pushed aside and did not cause further invagination until pressed against the cell wall. Fig. 2C presents similar evidence. Note that the host cell is plasmolysed and the haustorium turgid, this being evidence of the higher osmotic pressure of the latter.

Experiment VI

A VITAL HISTOPATHOLOGICAL STUDY OF THE DEVELOPMENT OF RESISTANT TYPE FLECKS IN VERNAL WHEAT

It has long been a controversial question whether the cells of a host highly resistant to rust die prior to those of the parasite because they are hypersensitive to some secretion of the fungus or whether the fungus dies first as a result of antitoxic action or of starvation. Because this information is requisite to a knowledge of the nature of resistance and might throw light on the significance of observed permeability changes a study was made of the histopathological development resulting from invasion of Vernal wheat (highly resistant to most races) by race 34.

Thin freehand sections of heavily inoculated leaves were vitally stained in neutral red; such sections were made and examined 18 hr. after inoculation and thereafter at several intervals during each successive day until flecks were macroscopically visible. The first examination (after 18 hr.) revealed that most spores had germinated, but only a very small proportion of germ tubes had gained entrance into the substomatal cavity. In about 30 hr. a number of germ tubes were observed each of which had passed through a stoma, had developed a short length of hypha in the intercellular space, and, coming into contact with a host cell wall, had formed a bulbous appressorial-like tip

which by septum development became cut off as a haustorium mother cell. At this stage there was no indication of injury to either the host or parasite. During the second day after inoculation very little advance was apparent. A few haustorium initials or small globular haustoria were observed, but there was still no sign of injury. On the third day the only change observed was the presence of a greater amount of mycelium. On the fourth day minute etiolate flecks were visible with a hand lens. These vestigial flecks were found to be due to the presence of small groups of cells having degenerate chloroplasts. Most of these cells were dead as indicated by lack of neutral red staining and by inability to plasmolyse. A few apparently retained an intact membrane, since neutral red would accumulate in the vacuole, but rupture of the membrane and sudden granulation of the protoplasm occurred on attempt to plasmolyse. All of these dead or moribund cells contained well developed haustoria. These haustoria were *still living* as indicated by the tests mentioned above. Some fields were observed in which a well developed haustorium, still living, was present in a dead cell, while a contiguous host cell with an haustorium in initial stages and coming from a branch of the same parent hypha that gave rise to the first haustorium, was still living. This suggests very strongly that, in Vernal, death of the host cells occurs prior to that of the fungus. A photograph of one such field is shown in Fig. 2E. It is regretted that the subjects are somewhat out of focus. This was inevitable since the mature haustorium and the second haustorium mother cell were in different focal planes. The paths of the hyphae are indicated by a dotted line.

On the fifth day after inoculation small flecks were readily visible macroscopically. A greater number of host cells near the centre of infection were killed. Cells that were near the edge of the mycelial zone and that contained initial haustoria were still living. The entire thallus seemed living, though hyphae in the region of killed host cells was more highly vacuolate than elsewhere. Fig. 2B is a photograph showing living mycelium ramifying through necrotic tissue while a cell at the edge of this zone and about to receive an haustorium is still alive. The resultant conviction from the many sections examined was, emphatically, that a fungus secretion leads to changes that cause death of the host cells some time before the parasite is itself injured.

General Conclusions

The author would prefer to extend and duplicate parts of these studies before making emphatic assertions relative to each experiment, but some general statements seem justifiable, especially in view of the fact that other duties preclude any possibility of the author being able to make further investigations in this field.

The importance of permeability increase in making nutrients available to an obligate parasite and so fulfilling one essential prerequisite to successful parasitism has been repeatedly demonstrated. Further evidence that all fungal organs remain external to living host protoplasts adds emphasis to this. That excessive modification of the host cytoplasm (or plasma mem-

brane), which initially is expressed by permeability change, tends to become fatal is indicated by the studies on browning and on the mesothetic reaction.

Additional evidence that permeability decrease is one factor tending to confer resistance is indicated by the examination of flecks from a mesothetic reaction, since the rust thallus seems first to enjoy a relatively congenial environment but is afterwards restricted in growth, probably by retention of solutes, and perhaps of water, by a decrease in host cell permeability.

Indication that relative availability of water is a factor playing some part in the determination of susceptibility or resistance in mature Hope plants is sufficient to warrant further investigation.

Permeability change induced by mechanisms other than by rust attack do not greatly modify rust reaction, probably because the highly specific mechanisms of the rusts quickly become operative and render the rusts largely independent of permeability changes induced by other agencies.

The diverse manifestations of resistance and susceptibility to rusts and the delicacy with which the determining factors are balanced, particularly in such extreme instances as that afforded by the mesothetic reaction of wheat, seem to point to the fact that some physiological factor that is essential for successful parasitism normally is operative over a narrow critical range. Small changes in the micro-environment seem able to influence this factor to the extent of modifying the relative compatibility of host and parasite. There is no new thought expressed in this rather abstract generality, but if permeability increase or decrease be, respectively, concomitant with susceptibility or resistance then it appears rational to seek for some change that modifies the structural nature of the plasma membrane. Amphoteric behaviour first seemed a field worthy of investigation in this connection, but the author was unable to deduce what seemed to be a valid hypothesis from a consideration of this topic. However, observation of living sections of rusted tissue over a period of several years left a conviction that extracellular rust enzymes might have a pertinent bearing. In a number of instances, some of which are reported in the foregoing experiments, extracellular fatty materials were observed as a sequel to rust invasion. Similarly, from time to time, there has been evidence of changes in the state of hydrophily of the host protoplasm. If these observations are considered in relation to the universal secretion of enzymes by parasitic fungi and to the supposed nature of the plasma membrane, then there may be some degree of probability in the suggestion that the rust fungus secretes at least two enzymes; one a protease and the other an enzyme capable of splitting lecithins from the lecithoproteins in the membrane, and for the sake of brevity herein called a "lipase". (The occurrence of minute, free globules of translucent, yellowish, fat-staining material reported above in rusted wheat leaves lends evidence in support of the presence of this latter enzyme.)

Host cell permeability may well be oppositely affected by these two enzymes which act upon such different materials of the protoplasm or its membrane. (Indeed, Ballentine and Parpart (1) state that permeability of

different species may be oppositely affected by a lipase, alone.) If, therefore, one or other of these enzymes, depending upon its immediate environment, be inactivated by some substance in the host cell, or probably in the plasma surface, then the cell permeability would be increased or decreased depending upon which of the enzymes was operative. A plausible mechanism of inactivation is the mutual precipitation of enzyme with some colloid in the cell or membrane. The factors that might modify such a system are sufficiently complex to account even for the "eccentricities" of rust reaction.

Acknowledgments

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STARCH CONTENT OF WESTERN CANADIAN WHEAT¹

BY W. J. EVA², I. LEVI³, AND J. A. ANDERSON⁴

Abstract

Determinations of starch content have been made on 140 samples representing the principal grades of wheat passing through the larger inspection offices in Western Canada during the first five months of 1942-43 crop year and the whole of each of the three preceding crop years. The analytical method employed was Clendenning's modification of the Mannich-Lenz procedure, and the standard error of the mean of duplicate determinations was 0.17. The mean starch content for all samples was 52.5% on a 13.5% moisture basis (60.7%, dry basis); the maximum value was 56.2% and the minimum 48.2%. The Garnet grades and No. 5 wheat were high in starch content. Durum and Alberta winter wheats were also high in starch, particularly in 1942. Grades 1 to 4 Northern, which comprise the bulk of the wheat marketed in Western Canada, had an average starch content of 52.5%; but the starch levels for these grades at Edmonton were consistently higher at 53.5 to 54.5%.

The war has increased the demand for industrial alcohol and it has become necessary to make wider use of raw materials other than molasses and corn. Wheat has attracted considerable attention because of the large supplies of it available on this continent. Considerable quantities have already been used by distillers in the United States, and a paper on the problems involved has just been published by Stark, Kolachov, and Willkie (5). They report, among many other observations, that the yield of alcohol is closely related to starch content, and that this varies widely among the various classes of wheat grown in the United States.

As it is probable that wheat will be used for making alcohol and other fermentation products in Canada, it appeared that a comprehensive study of the starch content of grades of Western Canadian wheat would prove useful. Hopkins (2, 3, 4) has reported on the starch content of some of these grades, particularly those of the 1933 and 1935 crops; the values obtained varied from 50 to 52% (13.5% moisture basis) for the hard red spring wheat grades; the Garnet grades were higher at about 55%. However there is no information on recent crops, or on variations in the starch contents of wheats originating from different parts of Western Canada. An appropriate set of samples have therefore been analysed in this laboratory, and the results are reported in this paper.

Materials and Methods

Average samples of all grades of wheat marketed in Canada are collected by the Inspection Branch of the Board of Grain Commissioners for Canada,

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and these samples were used for this study. They are collected during the grading process by throwing a handful of grain from each carlot sample into the appropriate bucket of a series covering all grades; the buckets are emptied each week; and, at the end of the crop year, the weekly samples are used to prepare a weighted average sample representing all wheat inspected during the year. Such samples as were available for all grades and classes of wheat (hard red spring, amber durum, and Alberta winter) inspected in the principal offices (Winnipeg, Edmonton, Calgary, Saskatoon, Moose Jaw, and Medicine Hat) in Western Canada during the first five months of the 1942-43 crop year, and the whole of each of the three preceding years, were collected for this study.

The analytical method employed was a modification of the Mannich-Lenz procedure developed by Clendenning for the determination of starch in whole wheat and wheat flour. This method, which is to be published shortly, is similar to the rapid method for starch in gluten (1) in that the protein dispersed by the calcium chloride solution is removed by precipitation with stannic chloride. In the present survey, 2.5 gm. samples were used, and the specific rotation of the starch was assumed to be $+200^\circ$. Until the modified method has been more widely used, it seems better to assume that the results are comparative rather than absolute.

The method was adapted to routine work by building a six-unit digestion rack provided with mechanical stirrers operated by a single drive shaft. The method calls for the use of *n*-octyl alcohol to reduce foaming, but in this laboratory supplementary control is obtained by arranging a nozzle over each beaker so that compressed air can be blown intermittently onto the foam.

The samples were ground in a burr mill and then reduced to a fine powder by ball-milling for 24 hr. Starch analyses were made in duplicate and in random order within the group for each crop year. Moisture tests were made by heating for one hour in an air oven at 130° , and all starch data are reported on a 13.5% moisture basis. The standard error of the mean of duplicate determinations was ± 0.17 , so that a difference of 0.49 between means of duplicate analyses represents the level at which the odds are 19 to 1 that a real difference exists between the means.

Results

The starch contents of the average samples of grades of hard red spring wheat are shown in Table I. Each of the first four sections of the table contains the data for a single crop year, together with mean values for each grade over all offices, and for each office over all grades. Both sets of means are weighted in accordance with the numbers of carlots represented by each individual sample. As the analyses were made in the middle of the 1942-43 crop year, the samples for that year represent only the inspections made between August 1 and December 31. In the bottom section of the table, the data are summarized as mean values over all four crop years.

TABLE I

STARCH CONTENT (%) OF AVERAGE SAMPLES OF THE GRADES OF HARD RED SPRING WHEAT

Crop year	Grade	Inspection office						All offices
		Win-nipeg	Cal-gary	Edmon- ton	Saska- toon	Moose Jaw	Medi- cine Hat	
1939-40	1 Northern	51.7	52.5	53.3	—	52.1	—	51.8
	2 Northern	—	51.5	53.3	—	—	—	52.4
	3 Northern	—	52.4	54.9	51.8	—	—	53.2
	4 Northern	49.6	52.3	—	—	—	—	50.4
	Number 5	—	—	—	—	—	—	—
	Number 6	—	—	—	—	—	—	—
	1 C.W. Garnet	—	—	54.2	—	—	—	54.2
	2 C.W. Garnet	54.0	54.8	53.3	—	—	—	53.8
	3 C.W. Garnet	53.5	54.4	55.5	—	—	—	54.6
	Mean, all grades	51.7	52.4	53.6	51.8	52.1	—	51.8
1940-41	1 Northern	53.1	53.2	54.5	52.1	50.6	50.6	53.1
	2 Northern	53.4	53.2	54.0	52.2	52.0	50.9	53.3
	3 Northern	—	53.1	54.4	51.9	52.1	52.6	53.0
	4 Northern	52.7	51.5	54.6	53.1	51.4	51.5	53.1
	Number 5	54.3	52.8	53.4	—	—	—	54.0
	Number 6	53.0	—	—	—	—	—	53.0
	1 C.W. Garnet	54.6	—	54.9	—	—	—	54.9
	2 C.W. Garnet	54.6	55.6	56.2	—	—	—	55.6
	3 C.W. Garnet	—	54.6	54.4	—	—	—	54.5
	Mean, all grades	53.2	53.3	54.5	52.1	51.9	51.0	53.2
1941-42*	1 Northern	52.9	51.6	54.0	51.6	49.9	51.4	52.8
	2 Northern	51.6	52.4	54.4	49.9	51.0	52.0	51.7
	3 Northern	52.4	52.9	54.2	51.6	51.6	53.4	52.6
	4 Northern	50.4	52.9	55.7	—	—	—	52.6
	Number 5	51.8	53.2	53.9	—	—	—	52.9
	Number 6	—	—	—	—	—	—	—
	1 C.W. Garnet	54.8	54.2	54.8	—	—	—	54.8
	2 C.W. Garnet	54.3	54.8	54.6	—	—	—	54.5
	3 C.W. Garnet	53.5	54.9	54.0	—	—	—	54.2
	Mean, all grades	52.2	52.3	54.5	50.4	51.0	51.8	52.3
1942-43 (First five months only)	1 Northern	51.7	50.7	54.4	51.0	—	52.2	51.8
	2 Northern	52.3	52.2	53.2	50.6	52.7	51.6	52.2
	3 Northern	52.6	53.9	53.9	53.5	52.8	52.9	52.8
	4 Northern	52.3	53.9	53.8	53.0	—	—	52.6
	Number 5	53.0	52.9	54.1	52.4	—	—	53.1
	Number 6	51.5	52.3	52.7	—	—	—	51.6
	1 C.W. Garnet	—	—	—	—	—	—	—
	2 C.W. Garnet	52.0	54.6	54.2	—	—	—	53.7
	3 C.W. Garnet	—	54.4	52.3	—	—	—	52.5
	Mean, all grades	52.3	52.3	53.7	51.1	52.7	52.0	52.3
All years	1 Northern	52.4	52.3	53.8	52.1	51.3	51.4	52.4
	2 Northern	52.3	52.5	53.9	50.8	51.7	51.6	52.3
	3 Northern	52.4	52.9	54.3	51.9	52.1	52.8	52.7
	4 Northern	51.1	52.3	55.3	53.1	51.4	51.5	52.3
	Number 5	53.5	53.0	53.6	52.4	—	—	53.5
	Number 6	52.0	52.3	52.7	—	—	—	52.1
	1 C.W. Garnet	54.6	54.2	54.4	—	—	—	54.4
	2 C.W. Garnet	54.2	55.2	54.3	—	—	—	54.4
	3 C.W. Garnet	53.5	54.5	54.8	—	—	—	54.5
	Mean, all grades	52.4	52.6	54.1	51.4	51.7	51.6	52.5

* Average samples of 1 Hard and No. 4 Special, inspected at Winnipeg, were available for 1941-42; they had starch content of 53.0% and 48.2%.

The mean starch content for all samples was 52.5% (60.7%, dry basis), and the individual samples covered a range of 8 units. No. 2 C.W. Garnet, inspected at Edmonton in 1940-41, had the highest starch content, 56.2% (65.0%, dry basis), and Winnipeg inspections of No. 4 Special, for 1941-42, had the lowest, 48.2% (55.7%, dry basis). In each year, the Garnet grades, which may conveniently be considered as a group, had the highest starch content; their mean value over all years was 54.4%, 2 units higher than the general mean. They were followed by No. 5 wheat which gave a mean value of 53.5%. In other respects there is little indication of a relation between starch content and grade.

Among the offices, Edmonton inspected wheat of highest average starch content, 54.1%; inspections at Winnipeg and Calgary had intermediate values, 52.4 and 52.6%; and inspections at Moose Jaw, Medicine Hat, and Saskatoon, had low starch contents, namely, 51.7, 51.6, and 51.4%. The spread between offices was considerably greater than the spread between years; the figures are 2.7 and 1.4 units respectively.

Data for amber durum wheat are given in Table II. This wheat is grown in southern Manitoba and southeastern Saskatchewan, and all of it passes through the Winnipeg inspection office. It generally represents no more than 2.5% of the total amount of wheat of all classes marketed in Western

TABLE II
STARCH CONTENT (%) OF AVERAGE SAMPLES OF THE GRADES OF AMBER DURUM WHEAT

Crop year	Grade	Winnipeg office	Crop year	Grade	Winnipeg office
1940-41	1 C.W. amber durum	52.6	1942-43 (First five months only)	1 C.W. amber durum	53.4
	2 C.W. amber durum	53.8		2 C.W. amber durum	55.6
	3 C.W. amber durum	54.0		3 C.W. amber durum	55.6
	4 C.W. amber durum	—		4 C.W. amber durum	54.3
	Mean, all grades	53.8		Mean, all grades	55.5
1941-42	1 C.W. amber durum	54.1	All years	1 C.W. amber durum	53.0
	2 C.W. amber durum	53.8		2 C.W. amber durum	54.1
	3 C.W. amber durum	54.0		3 C.W. amber durum	54.4
	4 C.W. amber durum	53.4		4 C.W. amber durum	53.8
	Mean, all grades	53.8		Mean, all grades	54.1

Canada. In each of the three years for which samples were available, the starch content of durum wheat was higher than that of hard red spring wheat; the differences between the two classes were 0.6, 1.5, and 3.2 units, for the crop years 1940-41, 1941-42, and 1942-43. The data for the individual grades show some evidence of a relation between grade and starch content, although No. 4 C.W. is out of line in all three years.

Samples of Alberta winter wheat were available for only the 1941-42 and 1942-43 crop years. The wheat is grown in southern Alberta partly on

irrigated and partly on dry land. Some of it is inspected at Medicine Hat, but a number of cars are routed directly through Winnipeg. This class of wheat generally represents less than 0.2% of all wheat marketed in Western Canada. The data given in Table III show that Alberta winter wheat is higher in starch content than hard red spring wheat; the differences for the two years were 1.3 and 3.2 units. As between the Alberta winter and durum wheats, there was little difference in starch content for either of the two years for which comparisons can be made.

TABLE III

STARCH CONTENT (%) OF AVERAGE SAMPLES OF THE GRADES OF ALBERTA WINTER WHEAT

Crop year	Grade	Inspection office		All offices
		Winnipeg	Medicine Hat	
1941-42	1 Alberta red winter	52.8	54.2	53.5
	2 Alberta winter	53.4	56.1	54.8
	3 Alberta winter	54.2	—	54.2
	Mean, all grades	52.9	54.4	53.6
1942-43 (First five months only)	1 Alberta red winter	55.3	55.7	55.5
	2 Alberta winter	55.5	55.6	55.5
	3 Alberta winter	—	—	—
	Mean, all grades	55.4	55.7	55.5
All years	1 Alberta red winter	53.5	54.6	54.1
	2 Alberta winter	55.1	55.8	55.3
	3 Alberta winter	54.2	—	54.2
	Mean, all grades	54.0	54.8	54.4

Discussion

The samples that were studied represent all carlots of a given grade inspected during the whole of a single crop year. However, they do not necessarily represent a single crop; for during the period under consideration large quantities of wheat, particularly of Grades 1 and 2 Northern, were carried over from one crop year to the next on farms and in country elevators; and carlots of old wheat, new wheat, and mixed old and new wheat, therefore came forward for inspection in each crop year. This mixing of crops undoubtedly reduced the spreads between the mean starch levels for different crop years.

The interpretation of the data for 1942-43 deserves special comment in view of the situation described above. The 1942 growing season was wet, with the result that the protein content of wheat was low, and the starch content was presumably high. But there is little indication of this in the starch data for hard red spring wheats because so much of the old crop, which was high in protein content and low in starch, came forward for inspection with the new crop. On the other hand, this did not happen with the durum grades;

they consisted of the 1942 crop only, and they therefore appear much higher in starch content than grades of hard red spring wheat. The same remarks also apply to the comparison with Alberta winter wheat. It seems safe to assume that, if comparisons could be made between the 1942 crops of the three classes of wheat, rather than between inspections from August 1 to December 31, it would be found that the spread between hard red spring wheat and the other two classes was closer to 1.5 units than to the 3.0 units indicated by the data.

The interpretation of the starch data is made easier by drawing on information on variations in the protein content of wheat accumulated in this laboratory during the past 15 years. In general, starch content and protein content are inversely related; grain that is high in starch content is low in protein content, and vice versa.

Among the hard red spring wheats, the Garnet grades will almost invariably be high in starch content because they are grown largely in northern Alberta where rainfall is normally high. No. 5 wheat will generally be high in starch content also; for it contains large proportions of immature, frosted, and sprouted kernels, and these types occur most often in the high rainfall northern areas where the season is short, and early frosts and wet harvests are more prevalent. On the other hand, No. 4 Special, which contains wheats of low weight per bushel drawn from drought areas, will be consistently low in starch content. No. 6 wheat occasionally contains large proportions of light wheat, but it may also be fairly plump and high in starch content. The remaining grades, 1 Hard and 1 to 4 Northern, contain much larger proportions of the crop, drawn from wider areas, and their starch contents must therefore be close to the average for the whole crop. Because the No. 3 and No. 4 Northern grades contain higher percentages of damaged kernels, and because damage is more likely to occur in the north, where starch content is generally higher, a consistent increase in starch content with each decrease in grade, and a spread of 1.0 to 1.5 percentage units between 1 and 4 Northern, can normally be expected in average starch contents representing any extended period of years. However, in individual years, a consistent relation with starch content cannot always be expected among the upper grades, 1 Hard and 1 to 4 Northern.

Alberta winter wheat, which is grown partly under irrigation and partly on dry land, but under a time schedule that permits it to escape intense summer heat, is probably consistently high in starch content. The writers would expect durum wheat, most of which is grown in southern Manitoba, under conditions of moderately high rainfall, to be intermediate in starch content between the upper grades of hard red spring wheat on the one hand, and Alberta winter and Garnet wheats on the other.

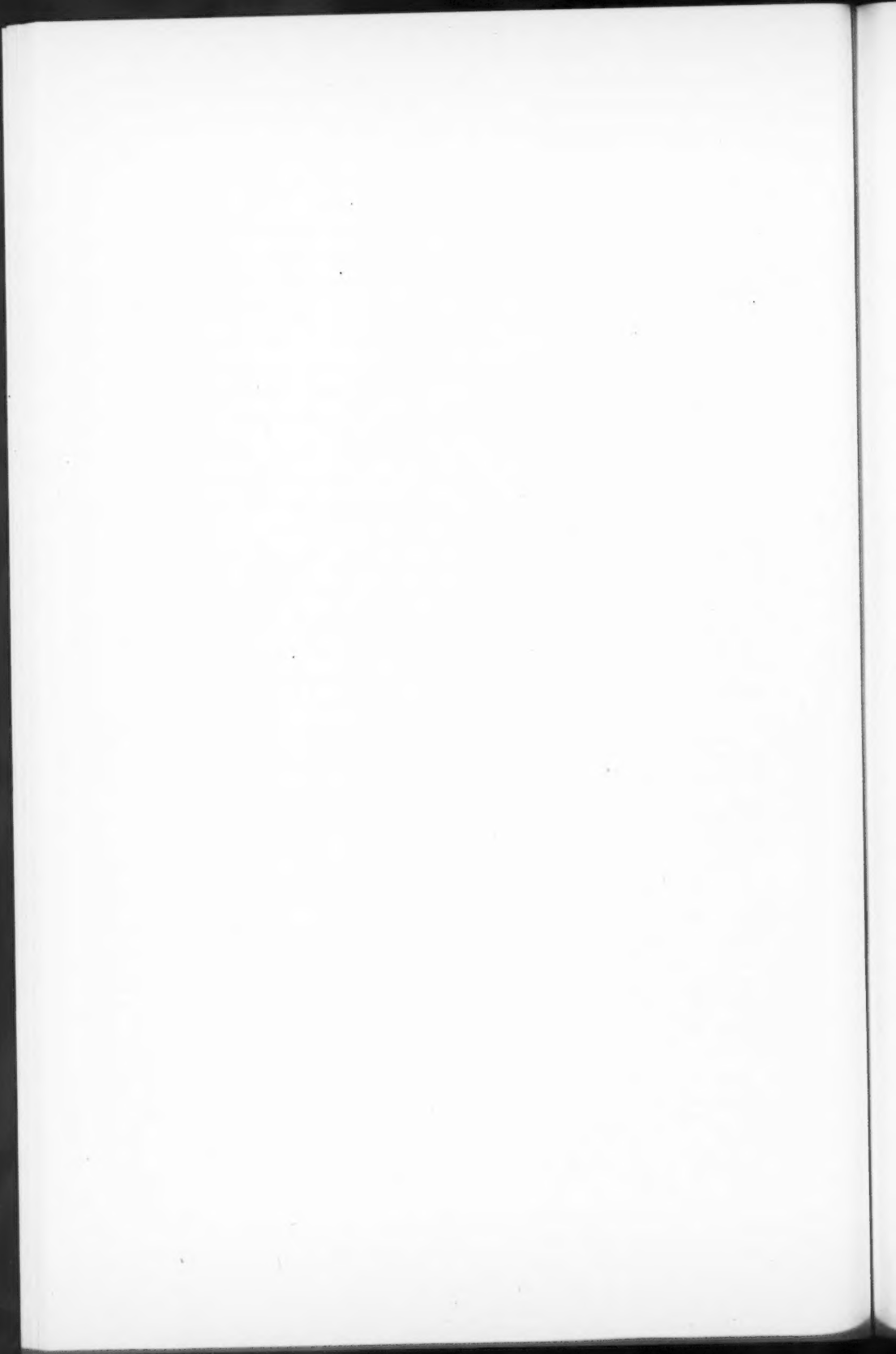
The amounts of wheat of classes and grades that are normally high in starch content will generally be small, particularly since a downward trend in acreages of Garnet and durum wheats has occurred in recent years. Distillers may therefore find it necessary to use the upper grades of hard red spring wheat. The data show, however, that the starch contents of these grades are higher at

Edmonton than at other inspection offices. The explanation is that Edmonton draws wheat from an area in which environmental conditions consistently tend to produce wheat of high starch content. All other offices serve areas in which growing conditions are more closely similar to the average for Western Canada as a whole. It will be noted, however, that low starch levels occur most frequently at Moose Jaw, Medicine Hat, and Saskatoon, and that the Calgary level is generally a little above average. The Winnipeg Office, which inspects over 80% of all the wheat marketed in the Prairie Provinces, and which draws wheat from a very large territory extending as far west as central Alberta, invariably has a starch level close to the general mean for all offices.

Data on the average starch contents of grades of wheat inspected at individual offices, such as those presented in this paper, do not present a complete picture of the variations in starch content that occur between carlots of western wheat. The samples represent averages of many cars, hundreds in almost all cases and thousands for the larger grades. Drawing again on experience with protein studies, we can safely assume that the maximum spread between carlots of any grade at any inspection office is just as great as the maximum spread between the average samples that have been studied. A spread of 8 to 10 units in starch content can confidently be expected. It follows that by judicious selection of individual carlots at Edmonton, or even at Winnipeg, it should be possible to obtain wheat of consistently high starch content for the production of alcohol in Canada. There is good reason to believe that the advantages to be gained by such selection will more than offset the difficulties involved.

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SOME NATIVE SAWFLIES OF THE GENUS *NEODIPRION* ATTACKING PINES IN EASTERN CANADA¹

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Abstract

The genus *Neodiprion* has become more and more important in recent years because of the variety of species found on our native conifers and the increasing frequency of outbreaks caused by these insects. It is very difficult to distinguish between the species by means of adult characters only, so a study of different stages of the life history has been made. In this way it has been found possible to delimit most of the species with a fair degree of certainty.

Keys are given for the determination of adult females of 11 and of larvae of 10 species attacking pines in Eastern Canada. Two of the species are described as new. The larvae of two species appearing in the first key and the adults of one species from the second are as yet unknown.

Introduction

During the past 15 years the sawflies of the genus *Neodiprion* have attracted an increasing amount of attention from forest entomologists in Canada. This has been due not only to the more common occurrence of damage to plantations and forests but also to the variety of species that has been found on our native conifers. This paper is an attempt to place on record a portion of the very considerable body of data relating to Eastern Canadian species that has now been accumulated, especially during the last four years, and to make possible the identification of the species that are likely to be encountered by forest entomologists and students of Hymenoptera.

Most of the field work on which this study is based was carried out at the entomological field station at Laniel, Que., where many of the species concerned have been reared from egg to adult. This was supplemented by further studies at Ottawa, where a certain amount of temperature control was possible and where methods have been devised for the rearing in incubators of most of the species concerned, although *N. pinetum* Nort. still presents difficulties. As a result of this work, good series of adults are available in most species, some series comprising several generations of descendants from a single pair. The field work has shown that the various species differ from each other in certain details of their life history, and that these differences can be used in separating them. Characteristics that have been used are

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larval coloration, spacing of eggs on needles, colour of cocoon, season in which adults emerge from cocoons, stage in which the winter is spent, gregarious or non-gregarious feeding habits of larvae. By a consideration of these characters it has been possible to segregate certain groups of individuals as representatives of true species; that is, it has been found that such groups behave as biological units. Once this has been done, it is possible to deal with adult material on a rational basis. In difficult and closely related groups such as these representatives of *Neodiprion*, it is practically impossible in some species to determine, from adult characters alone, the line between interspecific and intraspecific variation. However, when the range of variation has been examined in a series of adults that have been reared from larvae of a definite type and whose life history distinguishes them sharply from related groups of similar status, the taxonomic value of such variations can be evaluated. This "semi-genetical" method of attack has supplied the foundation for the present work and it is felt by the authors that many other problems in the taxonomy of forest insects can be solved only by similar methods.

The insects considered below include all the native species of this genus known to attack white pine (*Pinus Strobus* L.), red pine (*P. resinosa* Ait.), and jack pine (*P. Banksiana* Lamb.) in temperate Canada, east of the Manitoba boundary. No data are available for pitch pine (*P. rigida* Mill.) which is native to Canada only in very small areas along the extreme southern borders of eastern Ontario and New Brunswick (4). The species attacking western pines and those on other conifers have not yet been sufficiently investigated to yield material for a comprehensive treatment.

The writers have not included *Neodiprion abietis* Harr. among the pine feeders, although it has been recorded as one by some authors, including Bird (2) and Ruggles (23). They have been unable to find *abietis* on any pines in this region and all attempts to rear it from the egg on pines have failed. The female of this species, as understood by the writers, is readily distinguished (a) by the lancet of the ovipositor being unusually thickly haired, this area extending to the dorsoposterior margin and (b) by the scopal pad being shortly ovate.

With respect to hosts, it should be noted that the markings of larvae may vary within a species because of difference in host, as in *N. lecontei* (Fitch), but these variations are seldom, if ever, such as to place the specimen in the wrong section of the key, especially if larval descriptions are also consulted.

Identification of Adult Females

BY O. PECK

In 1918 Rohwer (18) erected the genus *Neodiprion** for the reception of numerous North American species and one European species (*sertifer* Geoff.), that had been referred previously to *Lophyrus* Latr. and *Diprion* Schr.; he

* *Diprion*, *Zadiprion*, and *Neodiprion* are words in the masculine gender, being derived from *πριων* (*prion*), masculine, a saw.

recognized two subgenera, *Neodiprion* (type *Lophyrus lecontei* Fitch) and *Zadiprion* (type *Diprion grandis* Roh.). Ross (22), in his synopsis of the nearctic genera of sawflies, considered these two groups as generically distinct, a course in which he was followed by Benson (1) in his synopsis of the diprionid genera of the world.

The genus *Neodiprion*, so limited, is readily separated from other nearctic genera of the Diprionidae by means of the characters tabulated by Ross (22). Unfortunately, the genotype (*lecontei*) falls in the first part of Couplet 1 of Benson's (1) key and hence does not run to *Neodiprion*. The character employed is the form of the anterior angle of the scutellum which is stated to be either much more than, or not greater than, a right angle. In *lecontei* the angle is about 115° (12, Plate 88; 22, Fig. 219), which is not exceptional since within the genus the angle varies from distinctly less than a right angle to about 115° . There is also some variation within certain species.

For the nearctic species of *Neodiprion* (s. str.) about 35 names appear to be available. To the genus belong all or nearly all of the species described in *Lophyrus* (s. str.) by Leach (11, pp. 120-121), Say (24), Harris (10, pp. 375-377), Fitch (8, pp. 58-60, 63-64), Norton (15, p. 225; 16), Cresson (5, p. 25), Dyar (7), and Rohwer (17). Other species have been described in the genus *Neodiprion* by Rohwer (18, 19, 20), Middleton (13, 14), and Schedl (24). Some of the larval forms have been dealt with by Yuasa (29).

Fortunately, almost all of the nearctic species were described from females. Only *N. edwardsi* (Nort.) and *N. hypomelas* (Roh.) were described from the male sex alone, and, as their types were taken in California and Colorado respectively, these species would seem to merit little consideration in this paper. In the present study, attention has been confined almost entirely to the females, a key being provided for this sex only.

The characters used for the identification of females by the earlier workers were size and colour, together with the number of antennal segments. Later workers described species in considerable detail, noting sculpture, shape of the antennal segments, and form of the scopal pad.

Relative size in the pine-feeding species is not of great importance since most of them are from 6 to 7 mm. long, their size being influenced by rearing conditions. However, *N. lecontei* is normally longer and more robust.

General colour is a character that should be used with caution, since yellow, ferruginous, red, piceous, and black tend to blend from one to another. However, *N. maurus* Roh. and *lanielensis* n. sp. form a distinct colour group, being almost entirely black. *N. lecontei* too is recognizable by the almost uniformly rufo-ferruginous colour of the dorsal areas in the prothorax and mesothorax. Colour pattern is of distinct value and is particularly useful in separating the two black species just mentioned, which differ in the pattern of the hind tibia.

Sculpture and punctation have to be used with great care, particularly so with respect to the head. Some variation occurs in the punctation of the

prescutum, scutum, and scutellum; however, the character is useful, particularly in *nanulus* Schedl, in which the scutellum is almost unpunctate, as in such species as *abietis* Harr. and *scutellatus* Roh.

Considerable variation occurs in the conformation of various areas in the head, notably the foveae, the frontal area, and the postocellar area.

As noted by Middleton (12, 13), the number of antennal segments in both sexes is subject to considerable variation. The form of these segments is of some value in separating species (18, 19, 20) but the characters are difficult to use.

The shape of the scutellum has already been discussed above. The tip of the anterior margin is often produced forward, although this character is not specifically stable. Rohwer (18, 19, 20) used the form of the posterior margin as a character, but the character appears to have little value in the species here reviewed.

The shape of the ninth sternum has been used by Rohwer (18) to differentiate certain species, but the character is of no value in our species.

As already noted, the shape of the scopal pads upon the apex of the ovipositor sheath has been considered by both Rohwer (18, 19, 20) and Middleton (13, 14) of great value in grouping species. By this character our pine-feeding sawflies fall into three distinct groups:

1. Species having the scopa much broader than the space between it and the inner margin of the sheath (*ferrugineus* Midd., *lanielensis* n. sp., *lecontei* Fitch, *nanulus* Schedl, *nigroscutum* Midd., *pinetum* Nort., and *rugifrons* Midd., with its variety *dubiosus* Schedl).
2. Species having the scopa about as wide as the space between it and the inner margin of the sheath, the pad more or less flat on top (*banksianae* Roh., *flemingi* n. sp., and *maurus* Roh.).
3. Species having the scopa about as wide as the space between it and the inner margin of the sheath, the pad sloping steeply away laterally, without a flattened apical area (*swainiei* Midd.).

Although the form of the scopal pad adequately serves as a means of grouping the species, yet some variation occurs in its proportions. This is particularly marked in *banksianae*, in which reared series have been studied.

The form of the ovipositor is valuable in identifying species. The shape of the lancet may vary specifically, that of *nanulus* being unusually slender and that of *flemingi* having the posterolateral margin straight rather than convex (Fig. 11). Although some intraspecific variation occurs in the shape of the lancet teeth, in their number within the rows, and in the number of rows of teeth, yet these structures are still of major importance in the recognition of species. Particularly useful is the ventral tooth of the second and of the third row of teeth. In the genus *Empria*, Ross (21) terms these ventral teeth *ventral lobes*. These lobes are enlarged, specialized teeth in *Neodiprion* too, the first occurring upon the first row of teeth that is ventrally complete (Fig. 11). The ventral lobes are sufficiently distinct in *maurus* and *nanulus* to permit these species being identified by these parts alone; usually it is necessary to supplement this character with others, particularly those of the scopal pad. In general, only a little variation occurs in the ventral lobes, except in *rugifrons* (s. lat.).

This evaluation of characters is based upon several thousands of specimens, nearly all reared from larvae. The bulk of these belong to *rugifrons*, *nanulus*, *banksianae*, *lecontei*, and *swainei*. Sixty-six female specimens of *maurus* were examined, 18 of *lanielensis* and 25 of *pinetum*, five of *nigroscutum*, and one each of *ferrugineus* and *flemingi*.

No attempt has been made to present the complete synonymy of the various species. The purpose has been to identify the *Neodiprion* species feeding on pines (particularly red and jack pine) in Eastern Canada.

KEY TO FEMALES

1. Scopal pad much broader than the distance between it and the inner margin of the sheath (Fig. 12).....2
 - Scopal pad about as wide as, or narrower than, the distance between it and the inner margin of the sheath (Figs. 13-15).....9
2. Scutellum smooth (very shallowly punctate at lateral and posterior margins); first ventral lobe of lancet large and subquadrate, the second a long and acute ventral tooth (Fig. 3).....*nanulus* Schedl (p. 114)
 - Scutellum coarsely punctate; first ventral lobe of lancet not unusually large but either dentate or triangular, the second not a long ventral tooth.....3
3. Head, prescutum, scutum, and scutellum uniformly rufo-ferruginous, immaculate, the prescutum and scutellum sometimes yellowish; species large and stout, usually much longer than 6 mm.; first ventral lobe of lancet more than twice as long as wide, with a coarse anterior tooth (Fig. 1).....*lecontei* (Fitch) (p. 115)
 - Head, prescutum, scutum, and scutellum not uniformly rufo-ferruginous, one or more with black; species not unusually large or stout; if first ventral lobe distinctly longer than wide (*pinetum*), then its anterior tooth slender (Fig. 6).....4
4. Body black (sometimes more or less piceous) with whitish markings; hind tibia entirely white; first ventral lobe of lancet not unusually long, the ventral margin sloping ventro-posteriorly (Fig. 10).....*lanielensis* n. sp. (p. 115)
 - Body extensively ferruginous, often with a large portion black.....5
5. First ventral lobe of lancet somewhat longitudinally rectangular, nearly twice as long as high, the anterior tooth long and slender (Fig. 6); lancet with eight or nine rows of distinct teeth.....*pinetum* (Nort.) (p. 118)
 - First ventral lobe weakly developed (Fig. 4), subtriangular (Fig. 9) or about as long as high, the anterior tooth coarse and short (Fig. 7).....6
6. Lancet ventrally emarginate at and behind the second row of teeth, the first ventral lobe weakly developed (Fig. 4); first lancet row with about four teeth, the second row with coarse and quite uneven teeth.....*nigroscutum* Midd. (p. 118)
 - Lancet ventrally not emarginate at the second row of teeth, the first ventral lobe well developed; teeth of second lancet row at least fairly even.....7
7. First ventral lobe of lancet small and equilateral, pointing ventrally (Fig. 9).....*ferrugineus* Midd. (p. 119)
 - First ventral lobe of lancet large, swollen posteriorly, ventrally straight or emarginate, anterodorsally toothed (Fig. 7).....8
8. Abdomen black or blackish.....*rugifrons* Midd. (s. str.) (p. 119)
 - Abdomen rufous or ferruginous.....*rugifrons* var. *dubiosus* Schedl (p. 119)
9. Scopal pad sloping steeply, the inner margin much higher than outer and meeting it at an angle of about 40° (Fig. 14); second ventral lobe bidentate, sloping anteroventrally (Fig. 8); prescutum fairly closely and evenly punctate.....*swainei* Midd. (p. 120)
 - Scopal pad with inner margin not much higher than outer, sometimes meeting at an angle of about 80° (Figs. 13, 15); second lancet lobe not bidentate, without an antero-ventral slope, except in *flemingi* (Fig. 11) which has the prescutum sparsely and unevenly punctate.....10
10. First ventral lobe of lancet subquadrate, swollen, nearly as high as long, with postero-ventral margin distinctly angulate (Fig. 2); body black with whitish markings, the vertex sometimes piceous.....*maurus* (Roh.) (p. 121)
 - First ventral lobe of lancet either the size of the second lobe or else much longer than high; body extensively reddish.....11

11. First ventral lobe of lancet rounded, about as high as long, not larger than the second (Fig. 11); scutellum coarsely and evenly punctate..... *flemingi* n. sp. (p. 121)
 First lobe of lancet rectangular, twice as long as high, much longer than the second (Fig. 5); scutellum with anterior portion sparsely, finely punctate.....
banksianae Roh. (p. 122)

Neodiprion nanulus Schedl

(Fig. 3)

Neodiprion sp., the black-headed jack pine sawfly, Schedl, Ann. Rept. Entomol. Soc. Ontario for 1930, 61 : 75, 1931.

Neodiprion nanulus Schedl, Z. angew. Entomol. 20 : 449-460, 1933; Mitt. deut. entomol. Ges. 6 : 41-44, 1935; Z. angew. Entomol. 24 : 51-70, 181-215, 1937.

Neodiprion sp. undescr., Brown, Ann. Rept. Entomol. Soc. Ontario for 1939, 70 : 98, 1939; ibid., Can. Dept. Agr., Ann. Rept. Forest Insect Survey for 1939 : 13, 19, 1940; ibid. for 1940 : 18, 1941; ibid. for 1941 : 14, 1942.

In 1933 Schedl (26) first used his names *nanulus* and *dubiosus* in a paper upon the application of Dyar's Law to these species and to *swaini*. Although Schedl evidently had no intention of validating these names, yet he did so by stating (a) that his two species were taken on *Pinus Banksiana* in north-western Ontario, (b) that both of his species had five larval instars and *swaini*, six, and (c) that certain statistical differences in the width of the head capsule occurred within each of the various instars of the three species. From the nomenclatorial viewpoint, this is sufficient to constitute differentiation between species and the names *dubiosus* and *nanulus* therefore are technically available, dating from 1933.

From the zoological viewpoint, this differentiation is entirely inadequate for the recognition of Schedl's species. Recourse must therefore be made either to the original material or to Schedl's supplementary papers.

All or nearly all of the original material was taken to Germany by Schedl. Should these specimens prove to be lost or otherwise unsuitable for lectotypes, some of his larvae, taken at Biscotasing, Ont., and now in the Canadian National Collection may be eligible. The adult "types", later described as such by Schedl (27), may be regarded as plesiotypes.

In the absence of type material, one should examine Schedl's other papers. From these it is evident that Schedl consistently considered that at Biscotasing there were known to him only three species of *Neodiprion* on jack pine. Two of these had pale-headed larvae (*swaini* and *dubiosus*) and early summer adults. The other had black-headed larvae and fall adults. The latter species was at first considered as apparently *banksianae* but later as a new species, *nanulus*. These data are in agreement with Schedl's plesiotype and with our present knowledge. While there is the possibility of his 1933 larvae being either *banksianae* or a species unknown to us, yet in the absence of type material, there are no reasonable grounds for doubting the correctness of Schedl's association of adult and larval forms.

Some systematists may regard Schedl's 1933 descriptions (26) as insufficient to validate the names *nanulus* and *dubiosus*. In this case, these names will still apply to the same species but date from 1935; the specimens designated

by Schedl (27) in 1935 as holotypes will then stand. However, this course of reasoning is to be deprecated as the term differentiation, as used in the International Code, must nomenclatorially be interpreted as broadly as possible, as in the past, lest greater confusion be created.

The species *nanulus* is easily recognized among the jack pine sawflies by its almost entirely smooth scutellum; the lancet too has the first lobe large and subquadrate and the second quite unusual as a sharp ventral tooth. The lancet usually has nine rows of exceptionally even teeth, but occasionally there are 10. Each lobe posterior to the third is in the form of a single tooth pointing anteroventrally and rounded ventrally.

The species is common and is to be found in Canada from the Maritime Provinces at least as far west as eastern Manitoba and from as far north as English River, Lake Abitibi, and Lake Saint John to as far south as Sarnia and the Eastern Townships of Quebec.

Neodiprion lecontei (Fitch)

(Fig. 1)

Lophyrus Lecontei Fitch, Rept. Noxious Insects N.Y. 4 : 58-59, 1859.

Lophyrus lecontei Fitch, Dalla Torre, Cat. Hymenoptera, 1 : 295, 1894.

Neodiprion (*Neodiprion*) *lecontei* (Fitch), Rohwer, Proc. Entomol. Soc. Wash. 20 : 84, 1918 (genotype).

Neodiprion lecontei (Fitch), Middleton, J. Agr. Research, 20 : 741-760, 1921; Yuasa, Illinois Biol. Monogr. 7(4) : 47, 1922; Twinn, Ann. Rept. Entomol. Soc. Ontario for 1934, 65 : 124, 1935; *ibid.* for 1935, 66 : 91, 1936; *ibid.* for 1936, 67 : 84, 1937; Ross, Illinois Biol. Monogr. 15(2) : 58, 151, 1937; Atwood, Can. Dept. Agr., Div. Forest Insects, Spec. Circ. Jack pine sawflies, 1938; Brown, Ann. Rept. Entomol. Soc. Ontario for 1937, 68 : 14, 17, 1938; Twinn, *ibid.* : 83, 1938; Reeks, *ibid.* for 1938, 69 : 26, 1938; Twinn, *ibid.* : 131, 1938; Brown, *ibid.* : 46, 50, 1938; Brown, *ibid.* for 1939, 70 : 97, 1939; Twinn, *ibid.* : 123, 1939; Benson, Bull. Entomol. Research, 30 : 340-342, 1939; Brown, Can. Dept. Agr., Ann. Rept. Forest Insect Survey for 1939 : 19, 1940; *ibid.* for 1940 : 19, 1941; *ibid.* for 1941 : 14, 1942.

The holotype of *lecontei* is in the United States National Museum and has not been seen by the writer. However, Middleton (12) has characterized the larval instars and the adults of this very distinctive species. The uniformly rufo-ferruginous colour of the head and of the dorsum of the thorax is diagnostic, as well as the stout and usually longer body. The lancet has 9 or 10 rows of even teeth, those of the first two rows, finer. The first row of teeth is long, almost reaching to the ventral margin of the lancet. The first three ventral lobes are angulate posteriorly (Fig. 1), the lobes beyond lacking the posterior angle.

The species is distributed throughout the length of the Appalachians, occurring as far south as Florida and Mississippi (12). In Canada, the species is to be found from the Atlantic coast to Lake Superior and as far north as Kipawa Lake, Que. in the Ottawa valley and Lake St. John, Que.

Neodiprion lanielensis n. sp.

(Figs. 10, 12)

Female. Length 7 mm. Head coarsely punctate; labrum sparsely, indistinctly punctate; clypeus with basal two-thirds irregularly, sparsely, and coarsely

punctate; apical third of clypeus smooth, somewhat depressed and broadly arcuate; median fovea small, round, fairly deep; vertex coarsely and sparsely punctate; vertical furrows distinct but not deep; postocellar area weakly arched, twice as wide as long, medially undepressed; antennae with 18 segments, third and fourth ones subequal in length and distinctly longer than wide at the base; antennal rami shorter than basal antennal width, the middle rami weakly emarginate in posteromedian view.

Thorax with coarse, irregular, and partially confluent punctation on mesoscutum and scutellum; mesoscutum laterally with much finer and closer punctation; angle of anterior margin of scutellum slightly obtuse, the apex not differentiated; scutellum posteriorly angular; cenchri separated by two-thirds of their own length; metascutellum closely, coarsely punctate, with precipitous anterior margin; mesoepisternum closely and coarsely punctate; hind basitarsus scarcely two-thirds as wide as long.

Abdomen shining, sparsely and indistinctly punctate; seventh sternum with emargination one-third as deep as wide, moderate in size; nates microscopically reticulate and very sparsely punctate; scopal pads three times as long as wide, flat above, inner margin subcarinate and separated from inner sheath margin by one-third the width of the pad (Fig. 12); lancet with 10 rows of uniformly large teeth; first row of lancet teeth long, reaching nearly to ventral margin of lancet; first ventral lobe of lancet anteriorly toothed and posteriorly swollen, the following lobes sharply pedate and pointing anteroventrally (Fig. 10).

Colour black; vertex with piceous spot lateral to vertical furrows; apical third of both labrum and clypeus yellow-brown; adjacent margins of second and third antennal segments dull yellow; palpi, apices of coxae and of femora, trochanters in part, tibiae, tarsi, and lateral stripe on abdomen pale yellow; apices of hind tibiae stained with ferruginous.

Male. Length 7 mm. In general agrees with description of female except median fovea larger, deeper, and longer; postocellar area more strongly arched; antenna with 20 segments; punctures of prescutum and scutum finer and closer; hind basitarsus slightly more than twice as long as wide. Colour black; labrum, clypeal apex, second antennal segment apically and tegulae apically, yellow-brown; vertex lateral to vertical furrows, black; legs ferruginous with coxae (except apices) black, the femora and hind tibia reddish; sternites strongly stained with red; hypandrium reddish ferruginous except the black base.

Holotype: ♀, Laniel, Que., 15-II-1941 (C. E. Atwood, 12140-92) reared on *Pinus Banksiana*; No. 5357 in the Canadian National Collection, Ottawa.

Allotype: ♂, same data except 18-II-1941.

Paratypes: Host *Pinus Banksiana*:—3 ♂♂, 1 ♀, Laniel, Que., 13 to 19-II-1940 (C. E. Atwood, 12140-92); 1 ♀, Petawawa Forest Reserve, Ont., 26-II-1940 (C. H. Zavitz, S. 133); 2 ♀♀, Laniel, 10 to 11-VII-1931 (M. B. Dunn). Host *Pinus resinosa*:—7 ♀♀, Laniel, 15 to 18-II-1941 (C. E. Atwood, 12136-

66); 1♂, 1♀, Laniel, 21-VI-38 (C. E. Atwood, 12111-8), both on same pin; 1♂, 1♀, Laniel, 15-II-41 (C. E. Atwood, 12136-76); 3♂♂, Norway Bay, Ont., 4 to 7-II-1941 (Forest Insect Survey 3152); 1♀, Red Pine Chute, P.Q., 16-I-42 (Forest Insect Survey 5104). Host probably *Pinus Banksiana*:—1♀, Mattawa, Ont., 4-II-1941 (Forest Insect Survey 2621). Host not recorded:—1♀, Bathurst, N.B., 18-VII (no year given), (J. N. Knull). Specimens emerging in January and February were incubated. Paratypes have been placed in the collections of the United States National Museum (Washington, D.C.) and of the Illinois State Natural History Survey (Urbana, Ill.). The remainder are in the Canadian National Collection.

Among the female paratypes certain colour differences were noted, these being the vertex entirely black, labrum piceous, clypeus apically ferruginous, mesoepisternum below tegulae yellow to piceous, hind tarsus and lateral abdominal stripe stained with ferruginous. The Bathurst specimen and one from Laniel (Dunn) have the whole of the vertex, of the pronotum, and of the mesoepisternum piceous. The form of the ventral lobes of the lancet varies a little. The male paratypes vary in colour somewhat similarly to the females, some specimens being much paler than others.

The females of *lanielensis*, being black with white markings, may be readily separated from the majority of *Neodiprion* species. The species with black females are *compar* Leach, *dyari* Roh., *eximius* Roh., *gillettei* Roh., *lateralis* Cress., *maurus* Roh., *mundus* Roh., and *pratti* Dyar.

The only description of *compar* is brief and is inadequate for recognition, although it agrees with *lanielensis* in the colour of the body, tibiae, and tarsi. The types are abroad. The type locality is Georgia, which is not sufficiently south to eliminate this species from consideration (*lecontei* has been recorded (12) as occurring as far south as Louisiana, Mississippi, and Florida). There is therefore a small possibility of *lanielensis* being a synonym of *compar*.

The names of the remaining species with black females can be eliminated with a very fair degree of confidence by using such characters in the descriptions as seem most stable. *N. dyari* is easily separated by its almost impunctate posterolateral margin of the prescutum (13 : 171), *eximius* by its ferruginous head (19), and densely punctate scutellum (14 : 79), *gillettei* by its flagellar rami being twice as long as the segmental width with the basal ramus the longest, *lateralis* by its femora being black (except at the apex), *maurus* as shown in the key above, *mundus* by the almost or entirely impunctate scutellum, and *pratti* by the larva having a pale head and feeding on cedar.

The writer has much pleasure in naming this species *lanielensis* in honour of those forest entomologists who studied the genus *Neodiprion* biologically at the Laniel laboratory in Quebec.

Neodiprion pinetum (Nort.)

(Fig. 6)

- Lophyrus le Contii* [sic] Kirkpatrick (nec Fitch), Ohio Farmer, 9 : 269, 1860 (fide Rohwer).
Lophyrus pinetum Norton, Trans. Am. Entomol. Soc. 2 : 328, 1869.
Lophyrus abbotti Riley (nec Leach), Ann. Rept. Insects Missouri, 9 : 29, 1877 (fide Rohwer).
Lophyrus pinetorum Dalla Torre, Cat. Hymenoptera, 1 : 297, 1894 (emend.).
Neodiprion pinetum (Nort.) Rohwer, Proc. Entomol. Soc. Wash. 20 : 87, 1918, (neotype); Yuasa, Illinois Biol. Monogr. 7(4) : 47, 1922; Middleton, Can. Entomol. 65 : 82, 1933; Brown, Ann. Rept. Entomol. Soc. Ontario for 1937, 68 : 14, 1938; ibid. for 1938, 69 : 46, 1938; ibid. for 1939, 70 : 97, 1939; ibid., Can. Dept. Agr., Ann. Rept. Forest Insect Survey for 1939 : 15, 1940; ibid. for 1940 : 24, 1941.

The type of *pinetum* has been either lost or ruined according to Rohwer (18), who designated for this species a neotype reared on white pine in Pennsylvania. The species is currently believed to be distinctive in its last feeding stage. The adults used in describing this species have been reared from such larvae.

The original description has been supplemented by Rohwer (18) and Middleton (14 : 82). The scopal pad is about three times as long as wide and is considerably broader than the space between it and the inner margin of the sheath. The lancet has been described in the key.

This species is not particularly common. In Canada it occurs north as far as Sault Ste. Marie, Lake Baskatong, Quebec City, and Gaspé, and south as far as Lake Ontario and the Bay of Fundy; it also has been taken in Newfoundland. Its Canadian distribution is rather similar to that of *lecontei*.

Neodiprion nigroscutum Midd.

(Fig. 4)

Neodiprion (*Neodiprion*) *nigroscutum* Middleton; Can. Entomol. 65 : 80-81, 1933.

The type material available for study consists of a single female paratype. The holotype was reared on jack pine at Biscotasing, Ont., by Schedl, the cocoon was spun on September 12 and the adult emerged on December 17. The holotype is labelled "Black head, type ♀", the colour presumably referring to the head of the larva. The Ottawa paratype emerged on December 18. From the two dates of emergence, it is to be assumed that the adults were incubated and would normally emerge in early summer; this is borne out by subsequent rearing data.

The species appears to be quite rare; indeed the writer has only seen four other specimens, all reared by Dr. J. W. M. Cameron at Chalk River, Ont. These emerged in an incubator in February.

The adults are distinct from the other pine-feeding species in the form of the lancet, its ventral edge emarginate at the second row of teeth, which is therefore without a ventral lobe. The lancet basally has the dorsal and ventral margins strongly divergent but this may not be a stable character.

Neodiprion ferrugineus Midd.

(Fig. 9)

Neodiprion (Neodiprion) ferrugineus Middleton; Can. Entomol. 65 : 82-83, 1933.

A single paratype of this species is available for study. The holotype labels bear the date "10. VII. 30", and "Type, brown ♀", the colour presumably referring to that of the larval head. The paratype at Ottawa has labels bearing the date "8. 6. 1930" and the word "row"; the latter refers to the method of oviposition. The type series was reared on jack pine at Biscotasing, Ont.

Although the data for the type series agree with the life history of *rugifrons* and although our single paratype does resemble that species, yet the difference in the shape of the first lancet lobe suggests that the species may be distinct. This lobe is small and triangular, without the coarsely rounded anterior tooth found in *rugifrons*. Considerable variation in the form of this lobe occurs in *rugifrons* but a lobe similar to that of *ferrugineus* has not been found in examining many reared series of *rugifrons*. The original descriptions of these two species do not differ sufficiently to permit confident separation of them. The names should, however, be kept separate for the present.

Neodiprion rugifrons Midd. (s. lat.)

(Fig. 7)

Neodiprion sp., the brown-headed jack pine sawfly, Schedl, Ann. Rept. Entomol. Soc. Ontario for 1930, 61 : 75, 1931.

Neodiprion (Neodiprion) rugifrons Middleton; Can. Entomol. 65 : 79-80, 1933.

Neodiprion dubiosus Schedl; Z. angew. Entomol. 20 : 449-459, 1933; *ibid.* Mitt. deut. entomol. Ges. 6 : 39-44, 1935; *ibid.*, Z. angew. Entomol. 24 : 51-70, 181-215, 1937; Brown, Ann. Rept. Entomol. Soc. Ontario for 1938, 69 : 46, 1938; *ibid.* for 1939, 70 : 98, 1939; *ibid.*, Can. Dept. Agr., Ann. Rept. Forest Insect Survey for 1939 : 13, 1940; *ibid.* for 1940 : 12, 1941; *ibid.* for 1941 : 8, 1942. **New synonymy.**

With considerable doubt, the writer has placed *dubiosus* as a colour variety of *rugifrons*, rather than as a distinct species. Up to the present the difference in colour has not been correlated with any stable morphological characters, although long series of reared material show a slight tendency for the two forms to merge. It is of interest to note that Schedl's plesiotypes included two specimens having the abdomen mainly black, although this was not mentioned by Schedl (27) in his notes on the variations in *dubiosus*.

The validity of the name *dubiosus* and its identity have already been discussed under *nanulus*, it being concluded that the name dates from the larval description of 1933 and that Schedl's series of adult "types" should be regarded as plesiotypes. The holotype of *dubiosus* not being designated, the interpretation of Schedl as the first reviser (28) has been accepted.

The holotype of *rugifrons* has not been seen by the writer but a paratype has been studied. The type series of *rugifrons* and the plesiotypes of *dubiosus* bear labels with unpublished data of importance. The holotype of *rugifrons* and the paratype at hand have Ottawa incubator labels recording the adult

emergence on Dec. 19, 1930, and a yellow label with "Row" or "Row type". The "holotype" of *dubiosus* and one other female of the series emerged on June 13, 1931, the other females on June 8, 17 (2), 26, 29, and July 1, while the two males emerged on June 8 ("allotype") and July 1. These data agree with the life history of *dubiosus* as given by Schedl (25, 28), in which the adults are described as emerging in early summer and ovipositing by the row method, their larvae being pale headed. The larvae of both series were taken by Schedl on jack pine at Biscotasing, Ont.

As suggested above, this species (or group) varies considerably in some morphological characters; these include the length of the antennal rami, the slope of the metascutellum, the proportions of the teeth of the tarsal claws, the dorsal profile of the base of the lance and the proportions of the first and second ventral lobes in the lancet. These characters, however, do not appear to be correlated with colour.

In Canada *rugifrons* (s. lat.) extends throughout the jack pine areas of Ontario and Quebec, as far east as New Brunswick and west to Prince Albert, Sask.

Neodiprion swainnei Midd.

(Figs. 8, 14)

Neodiprion sp., the jack pine sawfly, Dunn, Can. Dept. Agr., Div. Forest Insects, Spec. Circ. The jack pine sawfly, 1931.

Neodiprion sp., the twin-egg sawfly, Schedl, Ann. Rept. Entomol. Soc. Ontario for 1930, 61 : 75-76, 1931.

Neodiprion (*Neodiprion*) *swainnei* Middleton; Proc. Entomol. Soc. Wash. 33 : 171-174, 1931.

Neodiprion swainnei Middleton; Can. Entomol. 65 : 79, 1933; Schedl, Z. angew. Entomol. 20 : 449-459, 1933; *ibid.*, Mitt. deut. entomol. Ges. 6 : 44, 1935; Twinn, Ann. Rept. Entomol. Soc. Ontario for 1934, 65 : 123, 1935; *ibid.* for 1936, 67 : 84, 1937; Schedl, Z. angew. Entomol. 24 : 51-70, 181-215, 1937; Atwood, Can. Dept. Agr., Div. Forest Insects, Spec. Circ. Jack pine sawflies, 1938; Brown, Ann. Rept. Entomol. Soc. Ontario for 1937, 68 : 14, 1938; *ibid.* for 1939, 70 : 98, 1939; *ibid.*, Can. Dept. Agr., Ann. Rept. Forest Insect Survey for 1939 : 13, 1940; *ibid.* for 1940; 12, 1941; *ibid.* for 1941 : 8, 1942.

Although the holotype of this species has not been seen by the writer, yet available for this study were two male and three female topoparatypes. The type series was reared in the Mont Laurier district of Quebec Province, the host being jack pine and the collector M. B. Dunn. Although the original description of *N. swainnei* did not include the date of emergence, Dunn (6) reported this to be the latter part of June.

The females of this species are reddish and have a scopal pad that is unique among the species of pine feeders studied in this paper. These pads are three times as long as wide and slope steeply from each other; their adjacent sides are high and vertical as well as closer to the inner margin of the sheath than to the outer margins of the pad. The pads, too, are unusually well defined for they are distinctly raised above the level of the remaining, ridged portion of the scopa. The same general form of pad occurs in Maine specimens of *pinus-rigida* Nort. identified by Middleton. However, *pinus-rigida* is distinct in having its pad narrower, not more than a third as wide as the

distance between it and the inner margin of the sheath. In *swainei* the lancet has nine rows of teeth, the latter being unusually wide apart in the rows. The form of the ventral lobes (Fig. 8) is valuable in checking determinations.

In Canada this species has been taken as far north as Rimouski, Lake St. John, and the Kapuskasing River, east to the Maritime Provinces, west as far as southeastern Manitoba, and south to Sault Ste. Marie and Ottawa.

Neodiprion maurus Roh.

(Fig. 2)

Neodiprion maura Rohwer, Proc. Entomol. Soc. Wash. 20 : 89-90, 1918.

Although the type material of *maurus* has not been examined by the writer, this species seems quite distinctive. The type series of *maurus* was reared on jack pine in Wisconsin, close to Lake Superior; our Canadian material has the same host and also is found in the Lake Superior region.

This species is distinctive among our pine-feeders by the female being black with the hind tibia white but somewhat ferruginous apically. The other species of *Neodiprion* having black females have been discussed under *lanielensis* and can be separated from *maurus* by the same characters.

Our adults agree with the original description of *maurus* and show the same range of variation in colour. Other differences occurring among our series of females include the clypeus varying from black to almost entirely yellow, the hind tibia usually ferruginous with a longitudinal black stripe, and the postocellar area usually arched. Among the males the hind tibia is usually pale with a black anterior line. The lancet has sometimes 10 but usually 11 rows of teeth, those of the second and third rows uniform. The bloated form of the first ventral lobe (Fig. 2) is unusual, as are the lobes posterior to the third; each of the latter consists of an anteroventral, sharply acute, ventrally curved tooth.

In Canada the species has been taken in the triangle formed by a line from Kenora to Lake Abitibi and the upper St. Maurice valley, and extending south as far as the north shore of Lake Huron.

Neodiprion flemingi n. sp.

(Figs. 11, 13)

Female. Length 7 mm. Head sparsely, rather finely punctate; labrum shining, almost smooth; clypeus with apex broadly and somewhat angularly emarginate, shining; supraclypeal area coriaceous; median fovea small, circular; frontal area raised, flat, sparsely punctate, with faint and irregular rugulae; vertex sparsely punctate, vertical furrows subobsolete, postocellar area twice as wide as long and weakly arched; antennae with 17 segments; basal width of proximal flagellars slightly shorter than length of segment and slightly longer than length of ramus; ramus of basal flagellar shorter than the others.

Thorax dorsally shining; prescutum sparsely and finely punctate, scutum more closely so; scutellum uniformly covered with very coarse, separated punctations that are irregular in size and shape; scutellum with anterior margin forming scarcely more than a right angle, posteriorly rounded; cenchri separated by two-thirds of their length; metascutellum coarsely punctate, anteriorly with precipitous slope; mesoepisternum shallowly and discontinuously punctate; apical width of hind basitarsus equal to length of longer tibial spur and three-fifths the length of the basitarsus excluding pad.

Abdomen shining, impunctate except sparsely on the microscopically reticulate nates; seventh sternum with emargination three times as wide as deep; scopal pad three times as long as wide, as wide as the space between pad and inner margin of sheath; lancet with nine rows of teeth, the first ventral lobe anterodorsally and posteroventrally swollen.

Colour ferruginous; coxae, trochanters, base of tibiae, venter and lateral stripe of abdomen, whitish; labrum yellow; pronotum and scutellum yellowish-ferruginous; femora rufo-ferruginous; mesosternum posteriorly dark; metapleuron stained with black; antennae, dorsal and lateral margins of frontal area broadly, prescutum, scutum, and abdomen dorsally, black.

Holotype: ♀, Red Pine Chute, Kipawa, Que.; 5-II-1941 (incubator); collected by H. S. Fleming on *Pinus resinosa*; No. 5358 in the Canadian National Collection at Ottawa.

This species is described from a single female taken as a larva by H. S. Fleming and reared with sister larvae under the Forest Insect Survey No. 2705. After emergence from the incubated cocoon, the female oviposited on red pine. The larvae upon which the larval description is based were offspring of this specimen.

Neodiprion flemingi can be separated by this description from all of the adequately described species of the northeastern portion of North America. It can be distinguished from specimens of *N. americanus* Leach and from *N. dyari* Roh. (as determined by Sandhouse and Middleton, respectively) by the first ventral lobe of the lancet in the latter two species being longitudinally subquadrate rather than triangular. *N. flemingi* also appears close to *N. eximius*, which was reared from Wisconsin red pine, but the latter is distinguished by the densely punctate scutellum (14:79), the closely punctate prescutum, and the long spur of the hind tibia.

Neodiprion banksianae Roh.

(Figs. 5, 15)

Neodiprion n. sp., Graham, J. Econ. Entomol. 18: 337-341, 1925.

Neodiprion banksianae Rohwer, Proc. Entomol. Soc. Wash. 27: 115-116, 1925; Graham, Principles of forest entomology: 161-165, 1929.

Neodiprion sp., the black-headed jack pine sawfly; Schedl, Ann. Rept. Entomol. Soc. Ontario for 1930, 61: 75, 1931 (in part).

Neodiprion (*Neodiprion*) *ontarioensis* Middleton, Can. Entomol. 65: 83-84, 1933. **New synonymy.**

Neodiprion banksiana [sic] Rohwer; Middleton, Can. Entomol. 65: 83, 1933.

Neodiprion nanulus Schedl; Brown, Ann. Rept. Entomol. Soc. Ontario for 1939, 70 : 98, 1939; *ibid.*, Can. Dept. Agr., Ann. Rept. Forest Insect Survey for 1939 : 13, 1940; *ibid.* for 1940: 12, 1941; *ibid.* for 1941 : 8, 1942.

The holotypes of *banksianae* and *ontarioensis* have not been examined by the writer but a paratype of each species is available. The proposed synonymy is based mainly upon a study of long series of reared specimens, taken chiefly in Ontario and Quebec. According to Middleton (14), *ontarioensis* differs from *banksianae* in body size and in the number of antennal segments, as well as in the colour of the head, scutellum, and abdomen. However, reared series show that these characters vary sufficiently to account for the disagreements between the descriptions of Rohwer and Middleton for this species. The available paratype of *banksianae* differs from almost all of our Canadian specimens in being distinctly lighter in colour and in having a scopal pad slightly wider than the distance between it and the inner margin of the sheath; however, a few individuals from reared series agree with this paratype of *banksianae*.

Since no date of emergence has been published for the holotype of *ontarioensis*, it is pertinent to note here that according to a label on this specimen, the cocoon was spun on July 10, 1930; adult emergence would then occur in the fall. A second label has the words "black head, ♀", the colour evidently referring to the larva. These data agree with the biology of *banksianae*, as published by Graham (9).

The proposed synonymy is supported by the agreement of larval descriptions and other data of Graham with those of Atwood. Additional evidence is furnished by some Minnesota specimens (St. Paul, Sept. 1929, L. W. Orr), which agree in colour and scopal form with the common Canadian specimens. The type locality of *banksianae*, too, is Itasca Park, Minn.

The females of *banksianae* usually can be recognized by the pale general body colour, the coarsely punctate scutellum and by the usually elongate scopal pad which is about as wide as the distance between it and the inner margin of the sheath. The scopal pad usually is four to five times as long as wide and then is a distinctive character, but those few specimens in which the pad is proportionately broader should be examined to see that the first lancet lobe is longitudinal and that the lancet has 10 or 11 rows of teeth.

The species has been found in Canada to extend from New Brunswick to eastern Manitoba. It is one of our more abundant species.

Identification of Immature Forms

By C. E. ATWOOD

Larvae

The forest entomologist is more likely to encounter species of *Neodiprion* in the larval stage than as adults. Unless he can identify the larvae when found or at least before they spin cocoons, it is necessary for him to rear the insects to the adult stage, which may involve a delay of nearly a year, as well as a good deal of work, before he has any prospect of securing a name for

the insect. If the larva is parasitized or dies from some other cause, all the work will be lost and no name will have been secured. With these facts in view, the following key has been prepared in order to facilitate the identification of larvae in the field, using a hand lens, which in general is sufficiently powerful to show the characters used in the key.

In using the key, a certain amount of care is necessary in selecting material, since not only larval coloration but also the type of egg scar pattern and details of the seasonal life history have been used in the attempt to indicate the identity of each species. Therefore, larvae should be studied in conjunction with certain data that often are a necessary aid to their identification. The nature of these data will appear from the following sentences and from the key. In general, preserved material is hard to determine with certainty and living material should be used when possible. Even then, the key characters based on larvae alone are not always as reliable as could be wished, but fortunately, the larvae that resemble each other most closely in appearance are readily distinguished by the egg scar pattern characteristic of the species and by seasonal histories. The following rules may therefore be suggested in connection with the use of these keys.

1. Use living larvae in the last feeding stage, rearing them on the proper food if necessary, until that stage is reached.
2. When colonies are collected in the field, try to secure the needles bearing the eggs from which the larvae hatched.
3. Examine carefully each individual larva in a colony, as mixed lots are often found on the same tree or even on one branch.
4. If any doubt exists regarding the life history, keep cocoons spun by the larvae under proper conditions in order to find out whether the adults emerge in the fall or spring.
5. Until thoroughly familiar with the larvae of each species, confirm determinations by rearing adults and checking their identity by means of the keys and descriptions in this paper, or by submitting them to a specialist.

Knowledge of the life histories of these species is still very incomplete; many facts are not known at all, while tentative opinions on other aspects rest on insufficient evidence and must be verified or disproved by further work.

Oviposition and Seasonal History

The eggs, egg pockets, and oviposition habits of certain species of *Neodiprion* have been described by Middleton (12), Burke (3), and other authors. In general, the egg pockets are slits made in the edge of the needle by the ovipositor of the female sawfly and viewed from the side are roughly oval or shoe-shaped, the shape being somewhat variable for each species. However, it was found that each species makes a characteristic "egg scar pattern" because of the spacing of the eggs in relation to the length of the needle and that these patterns can sometimes be used as diagnostic characters for the species. The spacing of the eggs in the needle and on the tree also corresponds with the

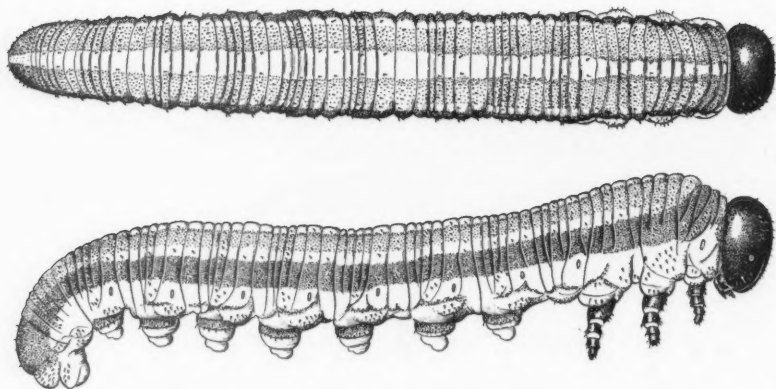
habits of the larvae in regard to gregarious or non-gregarious feeding. In general, each female lays all her eggs in a single clump of needles on one twig or on closely adjacent twigs, but some species do not do so.

KEY FOR THE DETERMINATION OF *Neodiprion* LARVAE

(Based on the last feeding stage and other details of the life history)

1. Subdorsal line consisting of a series of black or dark marks, distinctly separated from each other.....2
 Subdorsal line practically unbroken.....3
2. Head capsule predominantly black.....*pinetum* (Nort.) (p. 128)
 Head capsule orange to brown.....*lecontei* (Fitch) (p. 129)
3. Head capsule predominantly black, with or without lighter markings on frons and clypeus.....4
 Head capsule orange to dark brown (sometimes black in *swainei*), with or without dark markings on frons and clypeus; if head black, light posterolateral sutures and black patch on epiproct present.....9
4. Epiproct with a distinct black or very dark grayish blotch abruptly separated from subdorsal line.....5
 Epiproct without a distinct blotch; if darker than subdorsal line merging imperceptibly with it; head with posterolateral suture noticeably marked with lighter colour.....6
5. Black patch on epiproct usually with a distinct light median line for most of its length; dorsal line wider than subdorsal on abdomen; supraspiracular line usually broken, sometimes solid; a gray area between mesothoracic legs extending forward almost to prothoracic legs; larvae on trees in spring and early summer; pass winter in egg stage.....
 *banksianae* Roh. (p. 130)
 Black patch on epiproct with median line faint or almost absent; supraspiracular line composed of separate spots; dorsal line narrower than or subequal to subdorsal line on abdomen; area between meso- and prothoracic legs unmarked; larvae on trees in July and later; pass winter in cocoon.....*maurus* Roh. (p. 131)
6. Head in dorsal aspect marked with a light suture on each side of the posterolateral surface; clypeus and frons with a characteristic light colour pattern.....*laniensis* Peck (p. 131)
 Head in dorsal aspect without light markings.....7
7. Subdorsal and supraspiracular lines light green to light olive green, hypopleural lines almost absent; head with a pale spot at apex of frons.....*flemingi* Peck (p. 132)
 Subdorsal, supraspiracular, and hypopleural lines olive green, dark greenish gray or sometimes almost black; head without pale spot at apex of frons.....8
8. Lighter parts of body, especially in thoracic region usually dirty light grayish with little suggestion of yellow or green; darker stripes dull dark olive green; eggs laid in fall, scars usually separated in needle by their own length or more; larvae on trees in spring and early summer.....*nanulus* Schedl (p. 133)
 Almost identical in appearance with the above; lighter parts definitely light olive green or yellowish green, not grayish green; the whole appearance of the larvae, when alive, brighter green than *nanulus*; a grayish blotch on venter between mesothoracic and prothoracic legs; eggs laid in spring or early summer, scars separated by less than their own length; larvae on trees in July and later.....*Neodiprion* sp.* (p. 134)
9. Dark body markings usually black, very conspicuous, supraspiracular line often nearly solid; black mark on epiproct not sharply divided by a median line; cocoons when thoroughly soaked turn reddish or mahogany brown; eggs laid in rows, many per needle; larger.....*rugifrons* Midd. (p. 135)
 Dark markings often greenish or grayish, supraspiracular line almost never solid; black mark on epiproct divided by a light median line; cocoons remain buff or varnish yellow, seldom any suggestion of reddish; eggs laid one or two per needle, paired with those laid on other needle of the cluster (Fig. 52).....*swainei* Midd. (p. 136)

* Adults agreeing with female *N. ferrugineus* Midd., the only sex described, have not been reared. On the other hand, only eggs and larvae of the species in Couplet 8 of the key above, with *nanulus*, are known, and as the larvae were produced parthenogenetically by a female that was accidentally destroyed before it could be examined, the resulting adults were male only. When more larvae of this species are secured and reared so as to produce females, this species may prove to be *ferrugineus*.



TEXT FIG. Dorsal and lateral views of *Neodiprion nanulus* Schedl, V stage ♀.

Description of Larvae

In the following descriptions, the plan followed is that of Middleton (12, pp. 742, 743). For convenience of reference, a small part of his paper is quoted below.

"In the description of sawfly larvae, both structurally and for color, it is necessary that particular areas and regions of a segment or body wall be designated and that the designation adopted be applicable to both the thorax and abdomen of the larva in all its stages. Further, the method, or system, should permit by addition, elimination, change in shape, armature, and spotting of folds, areas, or regions, the comparison with other larvae, and at the same time should avoid possible confusion of meaning. The following is a suggestion for such a terminology and is the one used in the succeeding pages.

"An intermediate (second to eighth, inclusive) abdominal segment of *Neodiprion lecontei* consists of tergum, pleurum, and sternum and begins with the transverse tergal fold immediately preceding that above the spiracle.

"The tergum is composed of six transverse folds which are considered as representing four primary divisions (*A, B, C, D*), with one, the third, twice subdivided (*C^{1, 2, 3}*).

"The pleurum is divided into three folds—the dorsal anterior one here called the preepipleurite, the posterior one called the postepipleurite, and a ventral one called the hypopleurite—and two areas, one containing the spiracle and the other, armed with a few spines, posterior to and adjoining that containing the spiracle. The area containing the spiracle is at the lower extremity of fold *B* immediately above the preepipleurite and is termed the spiracular area, while the second area, that posterior to the above and armed with few spines, is below folds *C^{1, 2, 3}* and is termed the postspiracular area.

"The sternum consists of two transverse folds before the hypopleurites, one between and one behind them. The hypopleurites bear the uropods. . . .

"The interpretation of the segmental composition and terminology outlined above is applied to the thorax (Pl. 91, A,D) in the following way. Each of the three thoracic segments (prothorax, mesothorax, and metathorax) is 4-annulate tergally, and the annulations when viewed with reference to ornamentation, shape, position, and relation with one another homologize in order with the primary divisions (*A*, *B*, *C*, and *D*) of the abdomen, the third, *C*, not being subdivided.

"The pleurum is distinctly divided into four lobes, preepipleurite, postepipleurite, prehypopleurite, and posthypopleurite, in all three segments; and the postspiracular area is present, in approximately its relative abdominal position, in the mesothoracic and metathoracic segments, despite the absence or displacement of the spiracle.

"The sternum consists of three small, rather indistinct folds anterior to the leg's basal attachment to prehypopleurite and posthypopleurite.

"Further, the transverse circumference of the larva is divided into longitudinal areas of about equal width (Pl. 91, F).

TERGUM OR DORSUM

"The tergum or dorsum in the present paper is intended to designate that portion of the larva which is dorsad of the spiracular and postspiracular areas and which is divided into transverse folds or annulets *A*, *B*, *C*, and *D* in the thorax, and *A*, *B*, *C*^{1, 2, 3} and *D* in the abdomen.

I^a.—Middorsal, a single longitudinal midtergal line.

I.—Dorsal, a pair of longitudinal tergal regions, one to either side of the middorsal line.

II.—Subdorsal, a pair of longitudinal regions, one to each side of the dorsal regions.

III.—Laterodorsal, longitudinal regions, laterad of subdorsal regions.

IV.—Supraspiracular, longitudinal regions, laterad of latero-dorsal regions.

PLEURUM OR LATUS

"The pleurum or latus designates that portion of the larva between tergum and sternum.

V.—Spiracular, longitudinal regions, one to each side of the larva and ventrad of the supraspiracular regions, with the abdominal spiracle situated therein in most sawfly larvae, including *Neodiprion lecontei*.

VI.—Epipleural, longitudinal regions ventrad of spiracular.

VII.—Pleural, longitudinal regions ventrad of epipleural.

VIII.—Hypopleural or lateroventral, paired longitudinal regions, in which are situated the hypopleurites, one to either side of the sternum and ventrad of the pleural regions.

STERNUM OR VENTER

"The sternum or venter designates that portion of the larva beneath the body between the uropods. The ventrad projection of the uropods places them with reference to the position they occupy in relation to other structures in the adventral longitudinal areas.

IX.—Adventral, paired longitudinal regions containing the uropods, one protruding from each hypopleurite.

X.—Ventral, a pair of longitudinal sternal regions.

X^a.—Midventral, a single, midsternal, longitudinal line."

The descriptions below are based on the final feeding stage and the colours apply to living material except where otherwise stated. As noted elsewhere, it may not always be possible to identify preserved material by means of these keys and descriptions unless certain details of the life history are also known and every effort should be made to secure these when the larvae are collected.

Neodiprion pinetum (Nort.)

Head. Head capsule black, shining, with brownish areas at articulation of mandibles and on adfrontals; proximal third of clypeus dark brown to black, distal two-thirds straw colour marked on each side by a somewhat irregular blotch of black or brown which projects downward from the dark basal third; labrum dark reddish brown to black, mandibles black at base, reddish brown distally, other sclerotized portions of mouth parts reddish brown to black.

Thorax. Prothorax white or very pale yellowish, immaculate except for sclerotized sternal neck plates, prehypopleurites, and leg joints which are black or very dark brown. Meso- and metathorax with a subdorsal black spot extending over *A* and *B*, and a supraspiracular black spot on *B*, *C*, and the postspiracular area. Sternal regions as in prothorax with the exception, of course, of neck plates.

Abdomen. Same colour as thorax with the following markings: a black or dark brown subdorsal spot on *A*, *B*, *C*¹, and sometimes *C*² of segments one to nine, often obsolescent on some; a supraspiracular and spiracular black spot on *B*, *C*¹, *C*², and postspiracular area of segments one to nine, these spots darker than the subdorsal and persistent even when the latter are almost absent; epiproct with a black patch divided by a light median line.

Food Plants. Almost exclusively white pine in this region.

Oviposition and Seasonal History. Eggs are small, only three or four on a needle and the scars separated by more than three times their own length. Apparently all the eggs of each female are laid on a single twig and the larvae are gregarious; they appear on the trees during July and August and the mature larvae pass the winter in the cocoon among the litter under the tree.

Parthenogenesis. Nothing is known of the parthenogenetic behaviour of this species, and it has not yet been reared in the laboratory.

Neodiprion lecontei (Fitch)

(Figs. 19, 22, 25, 46)

Head. Head capsule orange-brown, with black spots surrounding the eyes; distal half of clypeus rather paler than capsule, especially at centre, but extreme distal edge bordered with darker brown; labrum often darker brown than head capsule, especially at margin; sclerotized portions of mouth parts pale yellowish brown to almost black.

Thorax. The thorax during life varies from deep yellow to pale whitish yellow and is marked as follows: prothorax immaculate above, sternal neck plates, prehypopleurites, and sclerotized portions of legs, black; on meso- and metathorax a subdorsal black spot on *A*, *B*, and *C*, diminishing posteriorly; a supraspiracular and spiracular black spot on *B*, *C*, and the post-spiracular area.

Abdomen. Similar in colour to thorax; a subdorsal black spot extending over *A*, *B*, and *C*¹ on segments one to nine inclusive; a supraspiracular black spot on *B*, *C*¹, *C*², and the dorsal part of the spiracular area; black patch on epiproct divided by a light median line. This description fits the great majority of the hundreds of larvae examined and differs from Middleton's description (12) in showing fewer black spots. Some specimens seen have a black spot on the epipleurites of all except the ninth abdominal segment and also on the meso- and metathorax. Very few have been seen with black postepipleural spots or with the black supraspiracular spot on the prothorax, noted by Middleton. Specimens are occasionally seen in which practically the whole abdomen except the epiproct is immaculate.

Food Plants. The favourite host is undoubtedly red pine, although jack pine is sometimes attacked. White pine foliage may be eaten by larvae that have migrated because of starvation but apparently eggs are not laid on it. In nature, only young pines in the open are attacked and larvae are seldom found on trees more than 15 ft. in height.

Oviposition and Seasonal History. The egg scars are made rather close together, separated by about one-third to one-half their own length. From 10 to 30 or more eggs may be laid on a single needle. All the eggs are laid as a rule on one twig and the larvae are very gregarious, feeding in dense clusters. Mature larvae pass the winter in the cocoon under duff and litter or in loose sandy soil, the latter apparently being preferred. Eggs are laid during June and larvae may be on the trees until late September.

Parthenogenesis. Large numbers of adults have been reared from virgin females; these have without exception been males. Some parthenogenetically produced families of larvae have been thought to be rather less vigorous than the sexually produced lots, but no proof of this opinion is available.

Neodiprion banksianae Roh.

(Fig. 51)

Head. Head capsule black, shining; central portion of clypeus slightly paler, whitish or greenish; labrum, mandibles and sclerotized portions of mouth parts black or very dark reddish brown.

Thorax. Pale greenish yellow to pale olive with the following markings: a subdorsal black line extending from Annulet C of the prothorax back on to the abdomen; a small gray spot slightly ventrad of the prothoracic spiracle; a large supraspiracular and spiracular black spot across the base of mesothoracic Annulets B, C, D, and the areas immediately adjacent ventrally; on the metathorax a similar spot often connected with the anterior spot by a few small dark spots on metathoracic A; neck plates and sclerotized leg joints black, and an irregularly shaped gray ventral area extending from between the mesothoracic legs forward almost to the prothoracic legs; this is sometimes obsolescent.

Abdomen. The subdorsal line is continuous with and similar to the thoracic; the supraspiracular spots are also similar; these may be separate or may be so large both on thorax and abdomen that they practically form a continuous stripe, in which case A as well as the other annulets bears a black spot. On the posterior thoracic and anterior abdominal region, the dorsal line is usually wider than the subdorsal, but is narrower on the prothorax and near the epiproct. Abdominal segments two to eight bear a subspiracular dark gray spot on the spiracular and postspiracular areas and the dorsal part of the pre-epipleurite, while on segments one to eight, the postepipleurite is largely black and the hypopleurite bears a gray spot. The epiproct bears a large black patch with a light median line usually dividing it for at least two-thirds of its length. Specimens are occasionally seen in which many of the dark lines and spots are obsolescent.

Food Plants. This insect is primarily a jack pine feeder. However, in a mixed stand of jack, Scots, and red pine near Spencerville, Ont., the Scots pine is now being attacked with some severity and several egg clusters have been taken on red pine. Larvae have been reared from these eggs using Scots and red pine respectively as food and normal adults emerged from the cocoons, no undue mortality being noted.

Oviposition and Seasonal History. This species usually lays three, four, or five eggs per needle, each scar being separated from the next by two to three times its own length, although variations occur. The full complement of eggs is usually laid on one twig and the larvae are gregarious. Shrubby trees on lake shores, rocky ridges, or other situations fully exposed to sun appear to be preferred for oviposition but even fully stocked, vigorous stands are not immune from attack. The larvae hatch in spring from eggs laid the previous fall and most of them are full grown by early July. About two months are spent in the cocoon.

Neodiprion maurus Roh.

This species is practically indistinguishable in appearance from *N. banksianae* Roh., the characters given in the key to larvae being the only ones discovered and these are so slight that some difficulty will be experienced in their use. The two species are, however, readily separated on the basis of their life history; any larvae with black heads, distinct spots in the supra-spiracular position, and a distinct black patch on the epiproct should be considered as possibly belonging to this species if taken on jack pine after July 1 in the general latitude of Lake Temiskaming. Fortunately the females are very different from those of *banksianae* and may be told at a glance from that species.

Host. This species has been collected in the field only from jack pine. As it has been rare, material for testing on other hosts has not been available.

Egg Scar Pattern. The eggs are laid three to six per needle; the scars may almost touch each other but are usually separated by a distance of one-fourth to three-fourths their own length. The full complement appears to be laid on a single twig and the larvae are gregarious. They feed during July and August and pass the winter in the cocoon.

Parthenogenesis. No experiments have been carried out because of lack of material. Production of eggs in the laboratory by this species has been meagre.

Neodiprion lanielensis Peck

(Figs. 28, 31, 34, 39, 40, 44, 50)

Head. Capsule black or dark brown with the following markings: a narrow, pale brown, greenish or cream-coloured line borders the occipital foramen and is produced a short distance along the sutures that extend dorsally from the lateral extremities of this foramen; two light spots of similar colour, roughly semicircular, also continuous with the light border around the foramen, are present on each side of the epicranial suture (Fig. 40). A light spot is present around the dorsal point of the frons and occupies part of the frons itself as well as adjacent areas of the epicranium. A whitish area with a sinuate dorsal margin occupies the ventral part of the frons, extends across the genae with short extensions dorsally along the frontal sutures, and is continuous with the narrow border of the occipital foramen. The antennae are usually just outside the dorsal edge of this light area. The clypeus is darkened along the dorsal margin with a darkened area projecting downward on each side and continuous with the dark upper margin. The central area and the latero-ventral portions of the clypeus are whitish; the labrum, mandibles, and sclerotized portions of the mouth parts are dark brown to black.

Thorax. The ground colour of the thorax is pale olive green or yellowish. A broad subdorsal stripe of a darker, brighter green, about the colour of a red pine needle, extends backward from Annulet C of the prothorax and is continued on the abdomen. A very faint narrow laterodorsal line with irregular

edges and similar in colour to the dorsal, extends often in an interrupted condition from *A* of the mesothorax on to the abdomen; ventrad of this again is a supraspiracular and spiracular line similar in size and colour to the subdorsal. Sclerotized parts of the sternum are dark brown or black, including the neck plates; on the prothorax two dark patches are present on each side dorsad of the neck plates and a grayish or greenish patch extends forward, diminishing anteriorly, from the mesothoracic and metathoracic prolegs. Two small grayish spots are also present between the prothoracic legs.

Abdomen. The subdorsal and supraspiracular-spiracular lines are continuous with and similar in colour to those of the thorax, and extend on to the epiproct without a break. Posterior to the metathoracic legs a grayish or greenish stripe runs with slight interruptions along the hypopleural areas between the uropods and across the postepipleurites and hypopleurites of each segment to the eighth, where it stops on the eighth hypopleurite. Coloration of the remaining portions of the abdomen is very similar to that of the lighter parts of the thorax. In preserved specimens, the green stripes fade to gray or brownish and the lighter parts to white.

This larva may be distinguished from any others known from this region by the bright pine needle green of the darker stripes and by the conspicuous light markings on the head, especially on the posterior part of the epicranium.

Food Plants. This species seems equally at home on red and jack pine.

Oviposition and Seasonal History. The egg scars are usually separated by less than their own length but seldom touch each other. On jack pine, four or five per needle is most common; on red pine, there is a tendency to lay them in two groups of four or five even when 10 or so are present on a single needle. The eggs are scattered widely over the tree or possibly over several trees, and the larvae are solitary or nearly so. They feed during July and August and pass the winter in the cocoon.

Parthenogenesis. Only males are known from parthenogenetic eggs.

Neodiprion flemingi Peck

(Figs. 18, 21, 24, 43, 47)

Head. Head capsule black, except for the following markings: a light yellowish or greenish spot at the junction of the frontal and epicranial suture; a pale greenish spot occupies the central part of the clypeus (Fig. 43).

Thorax. General colour dull pale green to greenish white, lighter anteriorly; broad subdorsal and supraspiracular stripes extend backward from Annulet *B* of the metathorax, faintly separated by a paler laterodorsal stripe. Sclerotized parts of legs, neck plates, and prehypopleurites black or dark brown.

Abdomen. Dorsal, subdorsal, laterodorsal, and supraspiracular stripes are continuous and concolorous with those of the thorax, becoming paler posteriorly; a slight grayish mark on postepipleurites of segments two to five, venter whitish or cream with a greenish tinge. Preserved specimens fade to a dull ochre.

This larva may be distinguished from any others known in the area under consideration by the paleness of coloration and lack of conspicuous body markings and by the characteristic markings on the front of the head (Fig. 43). It is most likely to be confused with the black-headed form of *N. swainei* Midd. (Fig. 38) or with *N. lanielensis* (Fig. 40) but the facial markings including the black labrum will serve to separate them; if observed in the field, the typical egg scars of *swainei* are an additional means of identification.

Food Plants. This species has been taken only on red pine, but larvae reared in incubators at Ottawa readily ate jack pine foliage.

Oviposition and Seasonal History. The only female whose oviposition has been observed laid 14 eggs on one needle, these eggs being rather close together. Eggs are probably laid in late June or early July; larvae are on the trees until late August or September and the adults pass the winter as larvae in the cocoon. Larvae are gregarious.

Parthenogenesis. Male sawflies have been secured from eggs laid by a virgin female.

Neodiprion nanulus Schedl

(Figs. 26, 29, 32, 45, 53, Text Fig.)

Head. Head capsule shining black; lower median portion of clypeus and a spot at each side lighter in colour; clypeus dark brown to black; mandibles and sclerotized portions of mouth parts dark reddish brown to black; adfrontals and adjacent parts of genae sometimes brown.

Thorax. Prothorax dirty white to pale grayish green (usually with very little suggestion of yellow in living specimens) with markings as follows: on Annulets *B*, *C*, and *D*, a continuous dark grayish green or dark olive green blotch extending from the dorsal line almost to the spiracle; small grayish spots sometimes present in spiracular and subspiracular positions; legs, neck plates, and prehypopleurite black or dark brown; a grayish area sometimes present between prothoracic legs. Meso- and metathorax with a dark stripe in subdorsal position continuous anteriorly with blotch on prothorax; a similar dark stripe in supraspiracular and spiracular area, both these stripes wider than the pale laterodorsal stripe; scattered small gray patches often present in spiracular and subspiracular areas; a grayish band extending from prothoracic to mesothoracic and from mesothoracic to metathoracic legs on each side; the central portion of the venter between the prothoracic and mesothoracic legs nearly always with a grayish mark.

Abdomen. The dark dorsal and supraspiracular stripes are continuous with those of the thorax extending without noticeable interruption on to the epiproct. A pale spiracular stripe, which may be wide or narrow, runs across the central part of the spiracular and postspiracular areas; ventral to this is a dark band which may occupy only the pleural area or may extend from the lower part of the spiracular area to the hypopleurites, with various spots and areas including usually the pre-epipleurites, still pale; this stripe usually stops on the eighth segment and is represented on the ninth only by a small gray

spot; a larger gray spot is usually present on the subanal fold and a similar one on the base of each hypopleurite.

Food Plants. In the Biscotasing-Chapleau area, this species appears to prefer jack pine for oviposition; at Laniel and Mattawa, red pine is preferred although colonies are frequently taken on jack pine. There appears to be no morphological difference between adults of the two populations and although the jack pine larvae are somewhat lighter in colour, this is possibly due directly to the effect of food. Both young and mature pines of both species are attacked, some of the heaviest feeding on red pine having been observed on trees 65 ft. or so in height.

Oviposition and Seasonal History. The egg scar pattern of this species is somewhat irregular. In general, eggs on red pine are separated by about their own length; on jack pine the interval may be somewhat greater or smaller. On both species there is a decided tendency toward irregular grouping, small groups of eggs and single eggs being common. Ten to 15 eggs per needle are commonly found on red pine; five to eight is a common number on jack pine. The females appear to often divide their eggs among several twigs and small groups of eggs, sometimes only one needle on the twig being attacked, are common. The larvae are gregarious during the early stages but tend to disperse when they reach the fourth. Eggs are laid in the fall, spend all winter on the tree and hatch in late May or June. Cocoons are spun very near the surface of the duff.

Parthenogenesis. All adults secured from parthenogenetically produced eggs have been males.

Neodiprion sp.

This larva is almost indistinguishable from that of *N. nanulus* Schedl. In life it is somewhat brighter green in colour; all the specimens examined lack the ventral gray spot between the prothoracic and metathoracic legs; the subanal spot is extremely faint or absent and the dark line in the pleural region is narrow and practically confined to the postepipleurites and the areas immediately anterior and posterior to them; this line has rather sharply defined borders and does not tend to stretch upward on the the pre-epipleurites and spiracular area. Preserved specimens thought to belong to this species should not be determined without supporting data.

Food Plants. This species is known only from jack pine.

Oviposition and Seasonal History. The eggs are laid very close together, most of them practically touching, five to eight per needle being a common number. The larvae are gregarious. Although field observation is lacking, all the available evidence shows that the larvae feed during July and August and pass the winter in the cocoon.

Parthenogenesis. The only family that has been reared was from a virgin female and from this lot four males have been secured.

Neodiprion rugifrons Midd.

(Figs. 16, 20, 23, 41, 42, 48)

Head. Head capsule bright orange to orange-brown, with black eyespots; antennae, and antennal sockets mostly brown; clypeus paler in centre, lower edge darkened; labrum usually concolorous with head capsule, with dark brown border; base of mandibles orange to brownish; tips of mandibles and sclerotized portions of mouth parts dark brown. Most specimens have darkened areas along the upper portion of the frontal sutures but not at the junction of the frontals and epicranial. The adfrontals are also darkened in many specimens.

Thorax. Prothorax yellowish green to light olive with dark markings as follows: a subdorsal black patch on Annulets *B*, *C*, and *D*; a supraspiracular patch on *B* and *D*, and a much larger supraspiracular and spiracular patch on *C*, frequently extending upward so that it becomes continuous with the subdorsal mark; a small subspiracular spot on the spiracular area, often extending on to the pre- and postepipleurite; leg joints and neck plates dark brown and a brownish or grayish patch just dorsal to the neck plates on each side. The subdorsal marks appear brownish in preserved specimens while the more ventral ones are black or grayish. A dark subdorsal stripe, continuous in front with the marking on the prothorax, extends the full length of meso- and metathorax. A supraspiracular spot may be present on *B*, *C*, *D*, and the areas immediately ventral or may extend completely across all annulets, forming a continuous stripe along the supraspiracular region. The light laterodorsal line between these two darker stripes is usually well-defined except on the prothoracic Annulets *B* and *C*, where it is sometimes partly interrupted by the dark markings.

A black spot is also present immediately in front of each meso- and metathoracic leg; it may extend anteriorly almost to the next leg.

Abdomen. The subdorsal dark stripe noted on the thorax continues uninterrupted across segments one to nine. The supraspiracular markings may be present as patches on Annulets *B*, *C*¹, *C*², and *C*³, with light areas on *A* and *D*, or may be practically continuous, with *B* to *C*² a deeper black than the other annulets. In either case, the patches may extend ventrally to the spiracular and postspiracular areas. A subspiracular gray patch is also present on the ventral portion of the spiracular and postspiracular area of each segment, the dorsal portion of the pre-epipleurite and adjacent parts of this region. The postepipleurite and the lateral portion of the transverse fold in front of the abdominal prolegs are black on segments two to eight; segment one has a less extensive black patch in the corresponding position while on segment nine these markings are absent. In dark specimens the patches may be so enlarged longitudinally as to form an almost continuous epipleural stripe. The epiproct carries a dense black mark with only a trace of a median line.

Food Plants. This species is known only from jack pine.

Oviposition and Seasonal History. The eggs are laid very close together, many almost touching, scars seldom more than one-half their length apart. Ten to 12 eggs per needle are not uncommon. The larvae are very strongly gregarious and when numerous feed in large clusters. They are on the trees during July and August and apparently grow much faster than *N. swainei*. Winter is spent in the cocoon.

Parthenogenesis. Large numbers of males have been reared from the eggs of virgin females; no females have been secured.

Neodiprion swainei Midd.

(Figs. 17, 35-38, 52)

Head. The head capsule colour and pattern in this species are variable, ranging from light orange to black. Four of these variations are shown in Figs. 35 to 38. The typical form has an orange or orange-brown head capsule, black eyespot, a brownish patch along each arm of the frontal suture near its junction with the epicranial; clypeus somewhat darkened at the upper and lower margin with a light central area and a light spot at each side, labrum orange-brown with a dark margin; mandibles orange at base, reddish brown at apex; sclerotized portions of mouth parts black or dark brown. In the forms with darker heads, the vertex and the labrum are usually darkest while the frons, clypeus, and genae retain light markings even in the darkest individuals. The short suture running from the posterolateral margin of the occipital foramen toward the vertex is outlined in a lighter colour than the surrounding portions of the capsule; in this detail the larvae resemble *lanielesensis* from which they are, however, at once distinguished by the black epiproct in *swainei*.

Thorax. Creamy yellow to light olive-green with the following marks: an olive-green, grayish or almost black subdorsal stripe running from Annulet C of the prothorax back to the abdomen; on the meso- and metathorax a supraspiracular dark spot on the base of B, C, and the dorsal portion of the postspiracular area; neck plates and sclerotized portions of legs black. The supraspiracular spots are often obsolescent and sometimes absent.

Abdomen. General colour similar to or lighter than that of the thorax; subdorsal stripe and supraspiracular row of spots continuous with those on thorax, the latter usually obsolescent at least on the middle segments. On the abdomen these spots when present occupy the bases of B, C¹, and C², sometimes extending to the dorsal portions of the spiracular and postspiracular areas. The epiproct bears a black patch separated into two portions by a wide and distinct median line.

Body coloration in this species is variable, especially in regard to the presence or absence of the supradorsal spots. In general, larvae with darker heads have a more greenish body colour and darker and more numerous spots. Larvae with black heads appear to be usually, if not always, males, but not all male larvae have black heads.

Food Plants. This species is known with certainty only from jack pine; one or two doubtful records of occurrence on red pine need to be authenticated by a competent observer.

Oviposition and Seasonal History. This species has a most characteristic pattern; the eggs are laid in pairs, one in each of the two needles which arise from a common base. The eggs are generally so spaced that each member of the pair occupies the same relative position on the needle (Fig. 52). In the field, they are laid only in new foliage, when the needles are about half grown. The full complement is generally laid on a single twig and the larvae are very gregarious. They are on the trees from July until October and pass the winter in the cocoon.

Parthenogenesis. Only males have been secured from the eggs of virgin females.

Summary

In Eastern Canada various species of sawflies belonging to the genus *Neodiprion* have been causing damage to the white, red, and jack pine through eating the needles. These sawflies belong to at least 12 species, some of which are rare and two of which are new to science. Keys and descriptions are provided for the recognition of the adult females and mature larvae. The sawflies are separable from each other also by their habits, notably those of oviposition, feeding, and overwintering.

Acknowledgments

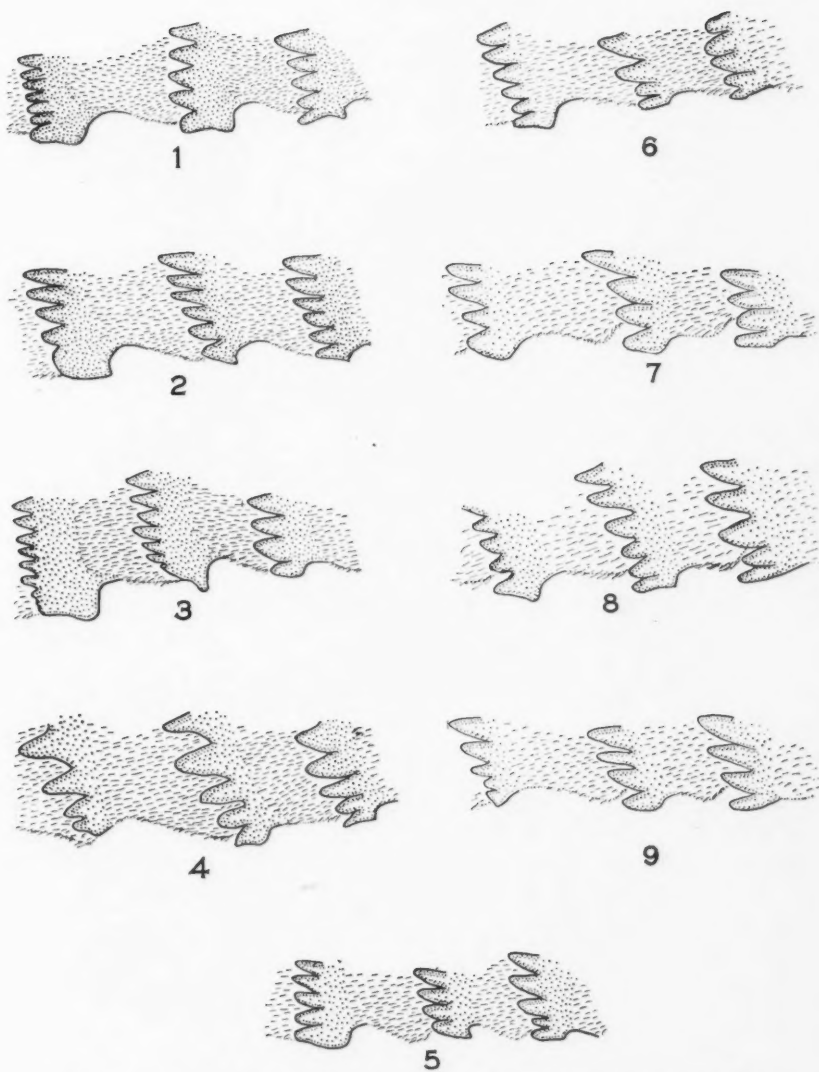
The writers wish to express their indebtedness to Dr. A. W. A. Brown and the staff of the Forest Insect Survey, who have aided in this work by supplying living material for rearing, pinned specimens, and data on distribution and food plants; to Dr. C. F. W. Muesebeck of the United States Department of Agriculture for supplying a pair of paratypes of *banksianae* and data in connection with certain types; to Mr. H. A. Richmond of the Entomological Laboratory at Winnipeg for supplying living larvae of one species; and to Miss Margaret MacKay of the Forest Insect Division for preparing figures of larval structures and egg scar patterns, with the exception of Figs. 1 to 15 which were drawn by O. Peck.

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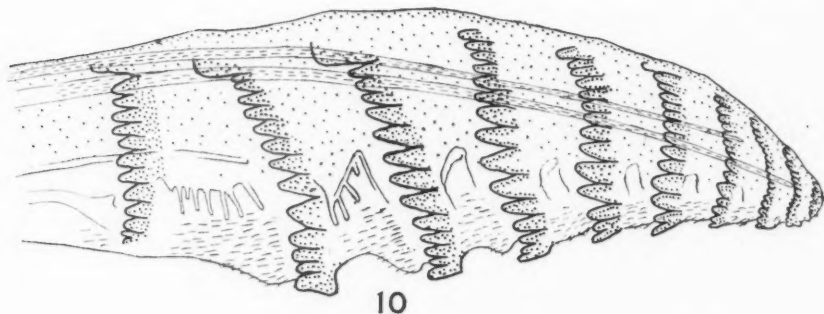
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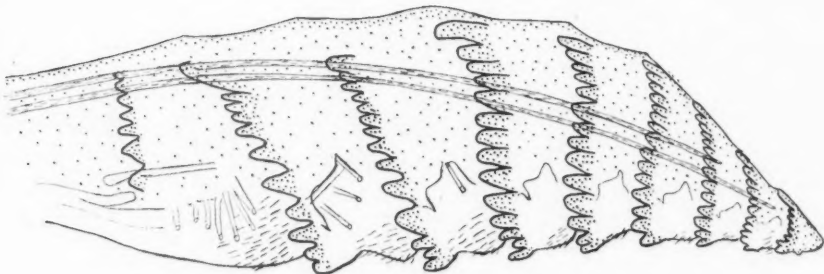
Note: Figs. 1 to 53 will be found on pages 139-144.



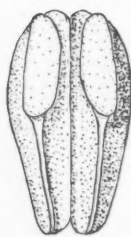
FIGS. 1-9. First, second, and third ventral lobes of lancet. 1. *Neodiprion lecontei* (Fitch). 2. *N. maurus* Roh. 3. *N. nanulus* Schedl. 4. *N. nigroscutum* Midd. 5. *N. banksianae* Roh. 6. *N. pinetum* (Nort.). 7. *N. rugifrons* Midd. 8. *N. swaini* Midd. 9. *N. ferrugineus* Midd.



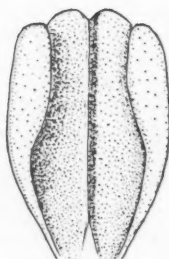
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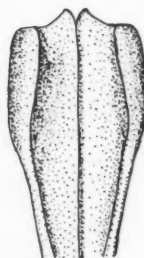
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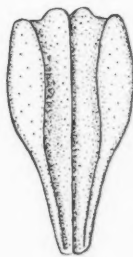
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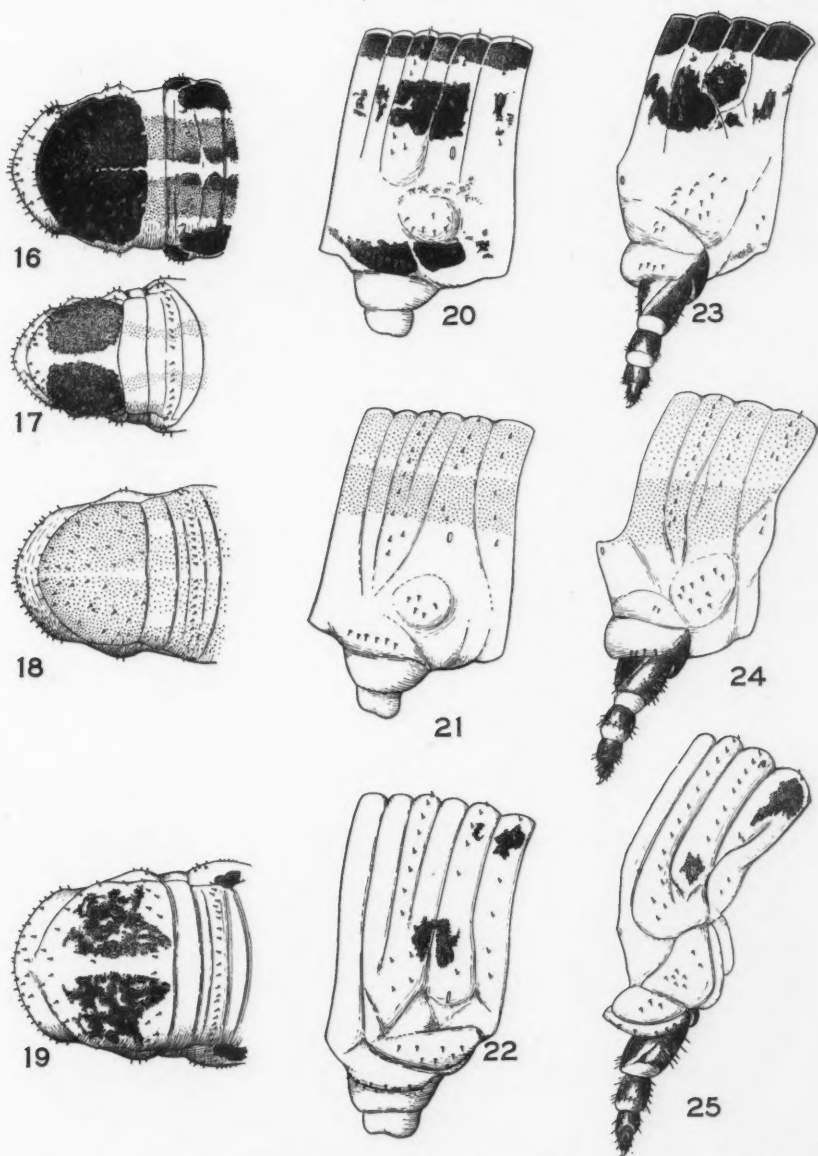


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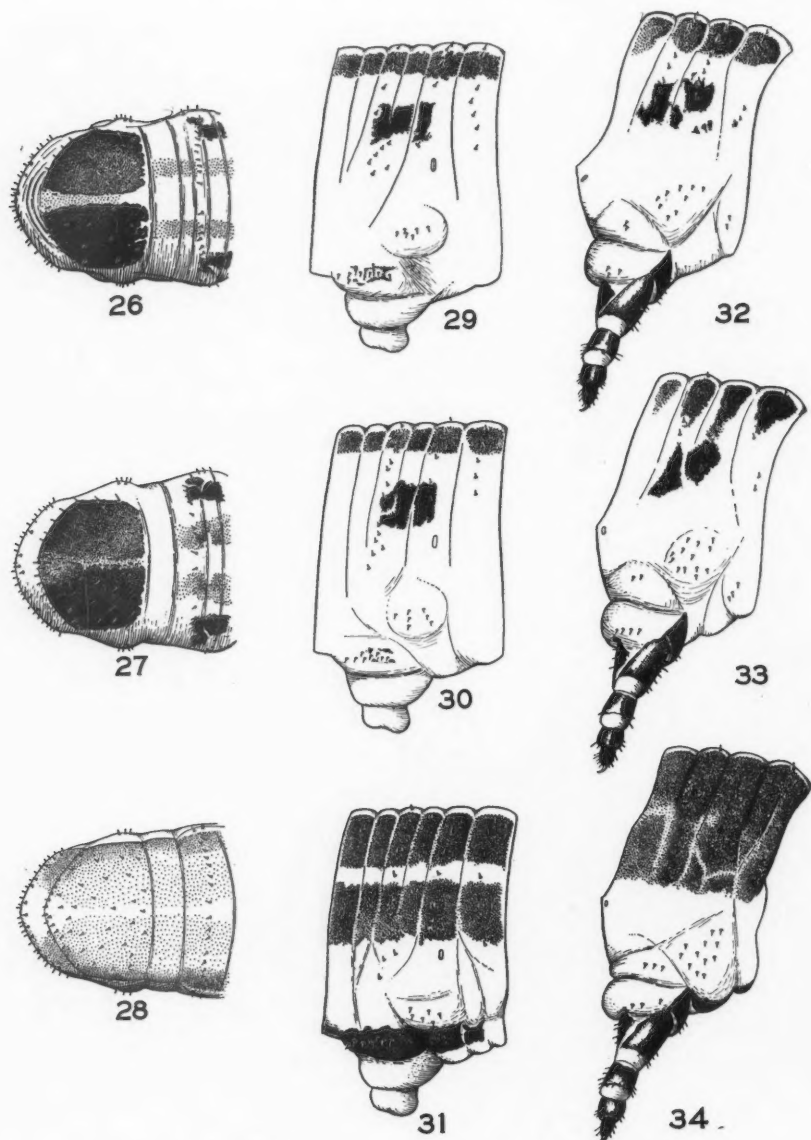


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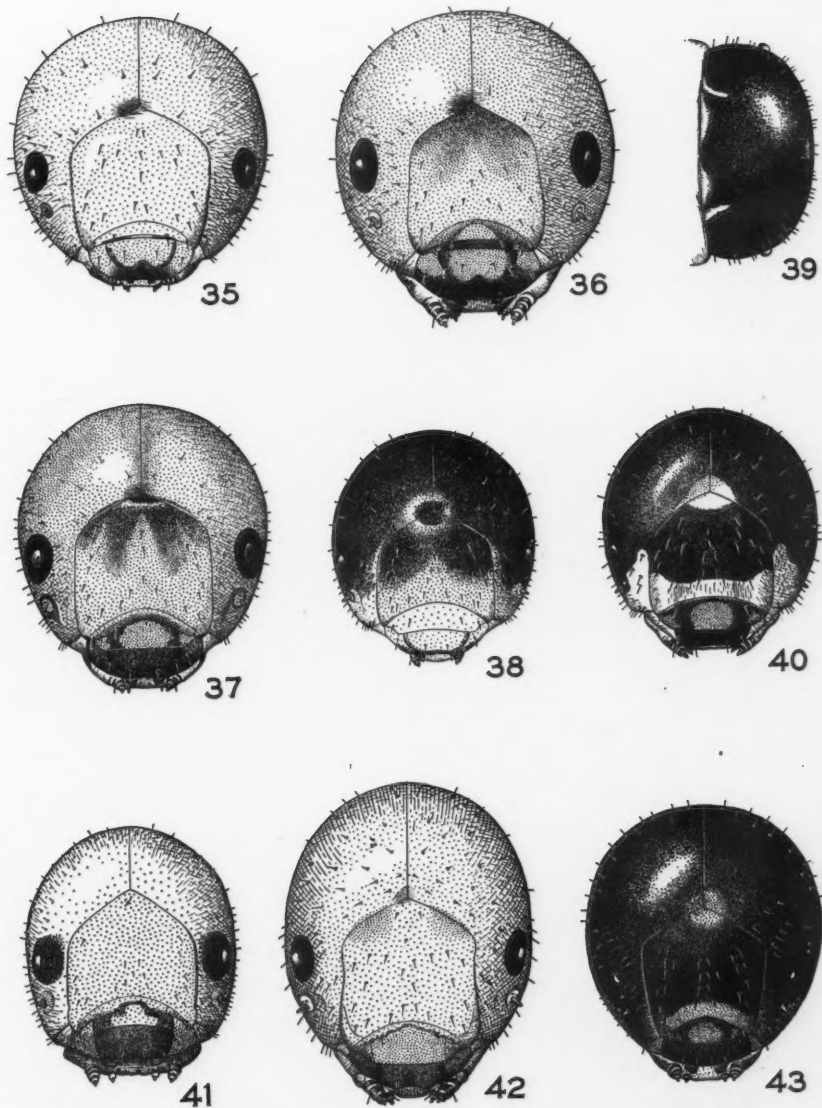
FIGS. 10, 11. Lateral view of lance. 10. *Neodiprion lanielensis* n. sp. 11. *N. flemingi* n. sp. FIGS. 12-15. Posterior view of scopa. 12. *N. lanielensis* n. sp. 13. *N. flemingi* n. sp. 14. *N. swaini* Midd. 15. *N. banksianae* Roh.



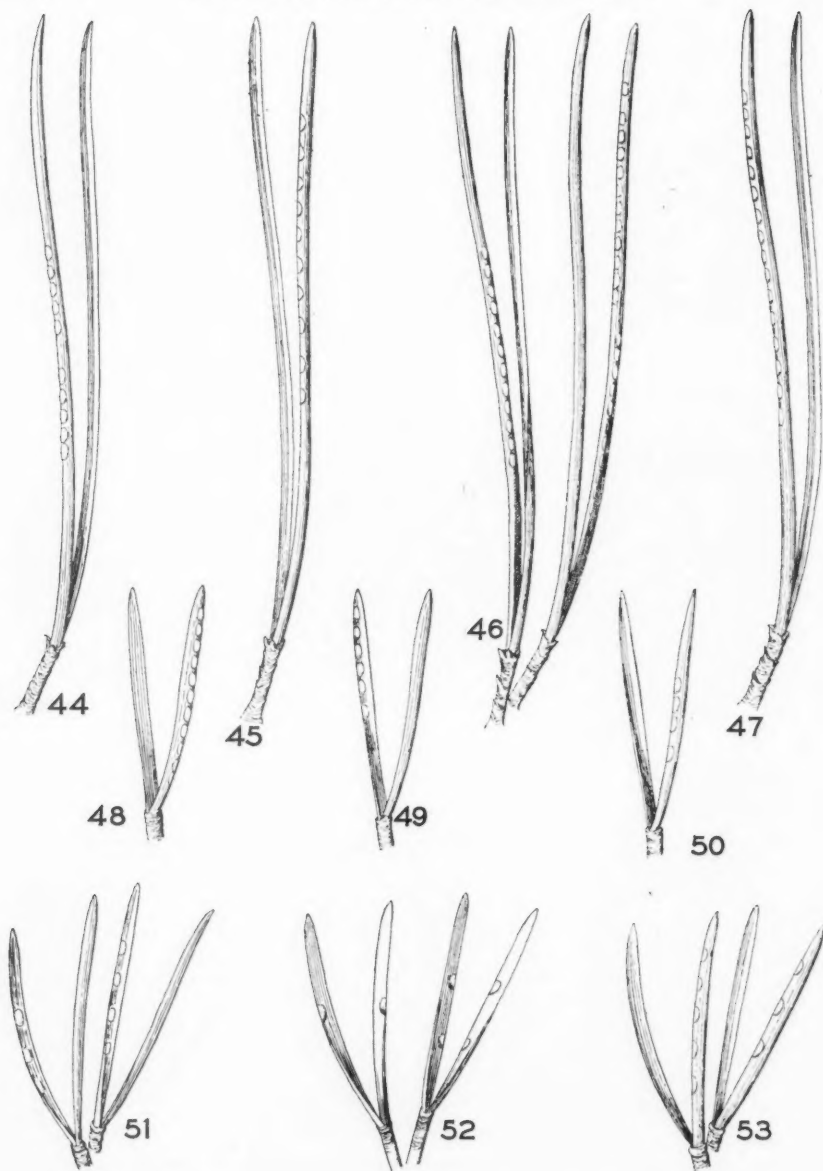
FIGS. 16-25. Larval colour pattern. Supra-anal area:—16. *Neodiprion rugifrons* Midd. 17. *N. swaini* Midd. 18. *N. flemingi* n. sp. 19. *N. lecontei* (Fitch). Typical abdominal segment:—20. *N. rugifrons* Midd. 21. *N. flemingi* n. sp. 22. *N. lecontei* (Fitch). Mesothoracic segment:—23. *N. rugifrons* Midd. 24. *N. flemingi* n. sp. 25. *N. lecontei* (Fitch).



FIGS. 26-34. Larval colour pattern. Supra-anal area:—26. *Neodiprion nanulus* Schedl. 27. *N. maurus* Roh. 28. *N. laniensis* n. sp. Typical abdominal segment:—29. *N. nanulus* Schedl. 30. *N. maurus* Roh. 31. *N. laniensis* n. sp. Mesothoracic segment:—32. *N. nanulus* Schedl. 33. *N. maurus* Roh. 34. *N. laniensis* n. sp.



FIGS. 35 - 43. Colour patterns of larval head capsules. 35 - 37. Variations in brown-headed forms of *Neodiprion swainei* Midd. 38. Black-headed form of *N. swainei* Midd. 39. *N. lanielensis* n. sp. (dorsal view). 40. *N. lanielensis* n. sp. 41. *N. rugifrons* Midd., II stage. 42. *N. rugifrons* Midd., V stage ♀. 43. *N. flemingi* n. sp.



FIGS. 44-53. Egg scar patterns. In red pine needles:— 44. *Neodiprion lanielensis* n. sp. 45. *N. nanulus* Schedl. 46. *N. lecontei* (Fitch). 47. *N. flemingi* n. sp. In jack pine needles:— 48. *N. rugifrons* Midd. 49. *N. maurus* Roh. 50. *N. lanielensis* n. sp. 51. *N. banksianae* Roh. 52. *N. swaini* Midd. 53. *N. nanulus* Schedl.

PROTEOCEPHALUS PARALLACTICUS, A NEW SPECIES OF TAPEWORM FROM LAKE TROUT, *CRISTIVOMER NAMAYCUSH*¹

By D. A. MacLulich²

Abstract

A new species of tapeworm, *Proteocephalus parallacticus*, collected from lake trout, *Cristivomer namaycush* (Walbaum), in Algonquin Provincial Park, Ont., is described.

A proteocephalid tapeworm, abundant in trout in Algonquin Provincial Park and collected from them during a survey of the parasites of these fish (9), did not correspond to any published descriptions (1-8, 10-14) and is therefore described as a new species. The field work was carried out under the auspices of the Ontario Fisheries Research Laboratory while the author was on the staff of Algonquin Park, and facilities for the laboratory work were provided by the Ontario Research Foundation by the courtesy of Dr. S. Hadwen and the Royal Ontario Museum of Zoology by Dr. J. R. Dymond, Director. Dr. George R. LaRue has kindly examined specimens and the description and has agreed that this form is not *Proteocephalus pusillus* (Ward) nor any other form known to him.

Description

The species described agrees with characters of the family Proteocephalidae, genus *Proteocephalus* Weinland and subgenus *Teleostotaenia* Woodland (14).

Strobila

The strobila vary in length, commonly up to 30 mm. (one specimen 82 mm.); the width may reach 1.5 mm. The dimensions of the *proglottids* at 7.5 mm. from the anterior of the worm = 0.38 mm. in length \times 0.80 mm. in width; at 30 mm. from anterior = 1.14 \times 1.06 mm.; at 80 mm. from anterior = 1.32 \times 1.37 mm. The *proglottids* may show no external evidence of segmentation or may be rounded with a sharp constriction between each.

Neck

The unsegmented part behind the suckers to the first segmentation groove varies from 1.7 to 7.5 mm. in length, average = 3.5 mm.

Scolex

The scolex is square or oblong in anterior view, 0.2 to 0.6 mm. wide. There are four functional cup-shaped acetabula or *suckers* which face usually forward and slightly outward; an inconspicuous, smaller, non-functional, apical fifth sucker is present in mature worms. The functional suckers are

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Contribution from the Ontario Fisheries Research Laboratory, Department of Zoology, University of Toronto, Toronto, Ont.

² At the time, on the ranger staff of Algonquin Provincial Park, Ont. Now in the Navigation Branch of the Royal Canadian Air Force.

circular in outline, the diameter of the opening being about 0.1 mm. The fifth sucker is rarely seen in living worms; it was not cup-shaped in any of the material examined but conformed to the contour of the apex of the scolex.

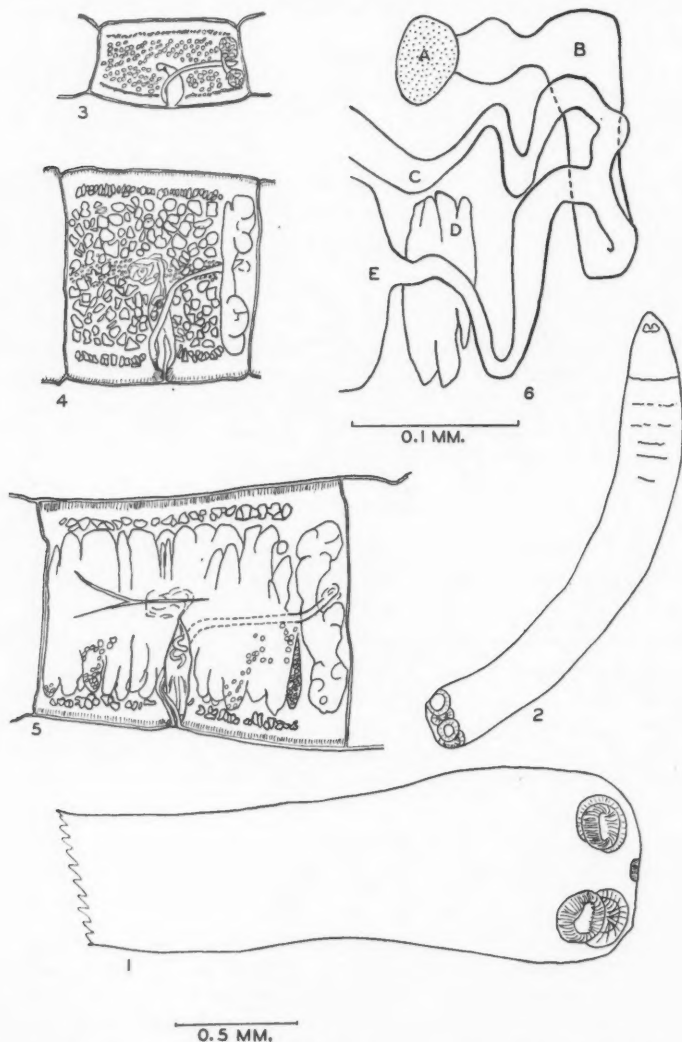


FIG. 1. Immature worm. FIG. 2. Scolex of mature worm. FIG. 3. Young proglottid, ventral view. FIG. 4. Mature proglottid, ventral view. FIG. 5. Ripe proglottid, dorsal view. FIG. 6. Connections of female genital system, built up from serial sections. Orientation: left = anterior, top = ventral. (A) = bridge of ovary, (B) = oviduct, (C) = vagina, (D) = oötype, (E) = uterus.

In stained and cleared mounts, this sucker is seen as an oval muscle mass with a basement membrane, the whole mass being 0.06 mm. in diameter, 0.03 mm. in thickness. The surface of the scolex between the acetabula varies from smooth to depressed, often with a pair of opposed grooves, resulting in a flattened cross section.

Genital Pores

The genital pores occur laterally at the midpoint of the segment, alternating irregularly from side to side; there is no papilla and the pore is usually in a depression.

Male Reproductive Organs

The *cirrus sac* is an elongate, pyriform pouch extending across more than one-third the width of the proglottid and nearly to the middle. The dimensions are 0.39 to 0.42 mm. by 0.11 to 0.14 mm. The *cirrus* is straight and cylindrical when invaginated and a slender cone with a blunt end when everted. The *ductus ejaculatorius* forms one to two, or rarely three, irregular coils within the inner half of the cirrus sac. The *vas deferens* consists of a small mass of coils in the centre of the proglottid, extending slightly anterior to the cirrus pouch, visibly connected to the ductus ejaculatorius but the tubules from the testes are rarely visible. The *testes* are somewhat flattened ovals in shape, in one irregular layer, a few overlapping each other. They vary in their three dimensions from 0.100 deep \times 0.081 \times 0.063 mm., to 0.120 \times 0.110 \times 0.076 mm. and average 0.11 \times 0.09 \times 0.07 mm. The number per segment varies from 45 to 92, the average number for 22 specimens being 71 testes per segment.

Female Reproductive Organs

The ovary is bilobed, the lobes quadrate, connected anteriorly by a slender bridge, becoming more irregular and lobulated in older proglottids. The *vitellaria* form a narrow line of small follicles down each side, inside the muscle zone, interrupted at the cirrus sac. They range in diameter from 0.045 to 0.065 mm. The *vagina* opens to the exterior dorsal to the cirrus sac and close beside it, within the depression or pit. The sphincter vaginae are insignificant and rarely seen. The vagina crosses the anterior portion of the cirrus sac obliquely—then passes ventrally across the part of the cirrus sac between one-half and three-fourths of its length from the exterior. The receptaculum seminalis, if present, is small; it may be entirely lacking. The vagina extends between the two halves to the rear of the ovary where it joins the *oviduct* which comes directly from near the bridge of the ovary. The oviduct leads forward again with a small amount of coiling to a rosette-like oötype and thence the *uterus* extends forward dorsal to the testes. In younger proglottids the uterus appears as a central column which in other segments is

hollow and in ripe segments is multilobed and fills much of the proglottid. The number of lateral pouches on each side of a segment varies from seven on the cirrus side and nine on the other to 10 and 12 and 13 and 15. The eggs are released by a splitting open of the body wall and uterus. The intra-uterine eggs measured 0.012 to 0.015 mm. in diameter.

Hosts

Specimens were found in the intestine of lake trout, *Cristivomer namaycush* (Walbaum), in speckled trout, *Salvelinus fontinalis* (Mitchill), and in brown trout, *Salmo fario* Linnaeus.

Material

The type specimen was collected from the intestine of a lake trout, *C. namaycush*, No. 96, in Lake Opeongo, Algonquin Provincial Park, Ont., Canada, on July 28, 1939. Slides and specimens preserved in alcohol are deposited in the Royal Ontario Museum of Zoology and two slides have been sent to the United States National Museum. Many other specimens from several hundred lake and speckled trout from various lakes in Algonquin Park were examined.

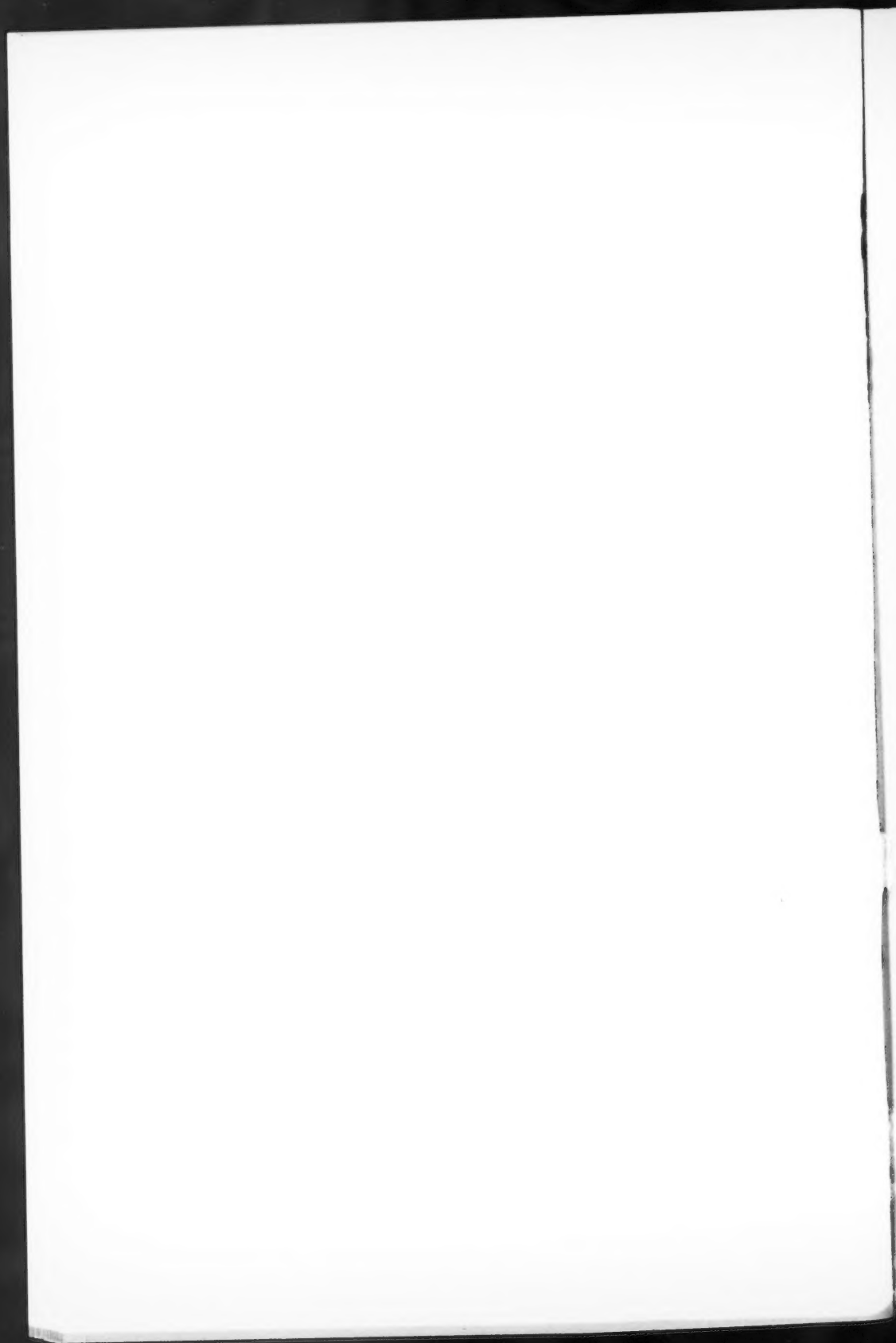
Discussion

The species name, *parallacticus*, refers to the manner in which the vagina crosses over the cirrus sac. The form described is distinguished from *Proteocephalus pusillus*, the only species with which it is liable to be confused, by the crossing of the vagina around and under the cirrus sac, which *never* occurs in *P. pusillus*. This is a prominent feature in whole mounts. Other differences, such as the larger size and number of some of the parts, are not of such positive diagnostic value as the above character.

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